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The vegetation ecology of a coastal, freshwater wetland

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The Vegetation Ecology of a Coastal, Freshwater Wetland

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from

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by

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Shrubs of the wetlands

Declaration

This thesis is submitted in accordance with the regulations of the University of Wollongong in fulfilment of the requirements of the degree of Doctor of Philosophy. The work described in this thesis was carried out by me and has not been submitted to any other university or institution.

Nicholas de Jong

January 1977

Summary

There is little known about the ecology of the freshwater wetlands on the south coast of NSW. Yet wetlands in the area continue to be lost, while others face increasing levels of human induced disturbance. At the same time there is an increasing local demand for information on wetland restoration and creation.

Coomonderry Swamp (34°48' S, 150°44' E) is, at 670 ha, the largest freshwater, coastal wetland in southern NSW, Australia. Partial National Park protection of the wetland followed recognition of its ecological significance in various inventories, although comprehensive surveys of the flora and fauna had yet to be carried out.

In this study the floristic composition and plant communities at Coomonderry Swamp were described. Comparisons were then made with a diversity of other local wetlands in order to investigate the distribution and abundance of key plant species over a broad range of conditions, to analyse characteristics of the environment responsible for determining plant species composition, and to assess the importance of Coomonderry Swamp as a reference site. The study progressed to an examination of vegetation change in response to the disturbance regime in Coomonderry Swamp and finally to an experimental investigation of the propagation and establishment characteristics of some key wetland species. Data from the various facets of research were used to compile ecological profiles of some important herbaceous wetland species.

Seven communities were defined by cluster analysis at Coomonderry Swamp with 11 'local variants' recognized within these. Plant community differentiation was considered to be related to the structure of vegetation, drainage and nutrient status of soils, and to disturbance and stress derived from anthropogenic influences and/or from flux in water levels. Cluster analysis of communities from eight other local wetlands resulted in the identification of a further four community types, with salinity being the major additional environmental component differentiating these groups from those described for Coomonderry Swamp.

The structure of vegetation along the elevation gradient at Coomonderry Swamp was broadly analogous to related toposequences for nearby upland

(plateau) wetlands and very similar to variations in structure described for coastal wetland systems of the central coast of NSW. However, floristic composition at Coomonderry Swamp differed markedly from that described for upland swamps. There were also substantial floristic differences between plant communities in standing water at Coomonderry Swamp and their equivalents in freshwater swamps of the central NSW coast.

Over 200 plant species were identified for Coomonderry Swamp and its humic soil margins. A number of these are rare or of regional significance. Some communities of the undisturbed freshwater margin, well represented at Coomonderry Swamp, such as native sedgeland and swamp mahogany open-forest, are regionally rare.

Aerial photographic records showed little change in the size and shape of Coomonderry Swamp over the past 50 years and only minor changes in the broad scale structure of vegetation. Zonations along both the herbaceous transition and the 'undisturbed' woody plant transition at Coomonderry Swamp were found to be spatially consistent and stable over the short term (three years).

Temporal dynamics within one region of herbaceous vegetation were investigated in detail. Wet meadow, at upper elevations, remained relatively constant in floristic composition despite small variations in the distribution and abundance of dominant species in response to inundation and seasonal flux. At lower elevations, more extreme conditions resulted in an alternation of communities between ephemeral meadow during drawdown and emergent stands, or open water upon reflooding.

Competition was hypothesized to be of increasing importance in determining floristics towards the drier, more mesic end of the herbaceous (wet meadow) transition. In particular pre-emptive competition limited the opportunities for establishment of transient species. Species richness in wet meadow was thought to be dependent on the fluctuating responses of dominant species such as *Pseudoraphis paradoxa* and *Isolepis prolifera*. This species pair showed significant temporal fluctuations in covariance. In my view, positive correlations suggested common responses when both species were previously limited (providing opportunities for transient species) while negative correlations suggested competition (excluding transient species).

Coomonderry Swamp is the only freshwater reference site on the south coast of NSW which supports a large number of indigenous wetland plant species. An experiment was carried out in previously cleared and grazed wet meadow at Coomonderry Swamp to investigate the establishment success of five key indigenous woody species under varying planting regimes. Planting of tube stock into uncleared vegetation was shown to be the most efficient and least environmentally damaging mode of establishment. Tube stock of all five species showed good growth over five months of frequent fluctuations in inundation, followed by four months of extreme drawdown. *Melaleuca ericifolia* plants remained robust over a subsequent 11 months, which included six months of constant inundation. Most *Melaleuca linariifolia* and *Casuarina glauca* plants also survived, but exhibited stress during prolonged inundation. Few *Eucalyptus robusta* plants (at the lower elevation) and *Leptospermum juniperinum* plants (at either low or high elevation) survived these latter conditions. Planting with seeds was not successful. Some seeds of all five species germinated, but no seedlings survived an episode of sustained inundation.

Clearing of plots for planting was found to have some adverse effects: robust weeds were introduced into the wet meadow and inhibited growth of three species, acid sulfate soils were exposed, and open, inundated plots were choked by algae. The experimental procedure proved valuable to other work at this site. For example, data were obtained on inundation and seasonal effects on weed versus indigenous invasion of cleared plots.

The research findings presented in this thesis should be further explored in a number of areas. Some south coast wetlands require further vegetation survey and the comprehensive floristic work at Coomonderry Swamp will need to be augmented by investigations of the fauna. Temporal monitoring will be continued at Coomonderry Swamp because there is potential for directional change in vegetation as anthropogenic threats increase. Ecological profiles of species will be modified with the accumulation of further data and the woody plant propagation methods will need to be tested at restoration sites.

Acknowledgements

In some types of ecological research one can lose oneself in an unexplored corner of Australia and never have cause to pass the time of day with a single soul. I soon learned that this was not to be the case with coastal wetland study. Liaison was required with land holders and a range of academic and government authorities. Without exception, I found these busy people to be friendly and helpful, and to be dedicated to a unified approach to wetland conservation.

I am indebted to officers and councillors of Shoalhaven City and Kiama Councils for their help. Graham Leonard, Ruth Devenney, Sandy Fritz, Howard Jones and Peter Stuckey took particular interest in my work. At various times assistance was provided by staff of the National Parks & Wildlife Service, the Lands Information Centre, the Bureau of Meteorology, the Department of Urban Affairs and Planning and the Department of Land & Water Conservation. A special thanks to Noel Kesby (Land & Water Conservation, Wollongong) who assisted me with soil testing.

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Keith and Cameron Stevens, Jim Hill, and Gavin Rogers allowed me to work on their properties and took a keen interest in proceedings.

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Roger Carolin, Rob Whelan and Joy Zedler provided comments on a draft manuscript based on Chapter 2 of this thesis, which has been accepted for publication.

Agaath de Jong prepared the water colour pencil drawings prefacing each chapter. Thanks Mum.

The most important task of a PhD student is to find the right supervisor. I found Rob Whelan when I was an Honours student and I didn't relinquish my hold. He expected organization and required a high standard of work. In return he gave friendship, leadership and always quality advice.

For many years Merridee de Jong has parented and worked while I studied. Despite the additional burdens, Merridee has been unfailing in her encouragement and interest. There are some signs that my research has influenced our children to care and be interested in the environment and to see the value of the learning process. If this is the case, then I have repayed Merridee in a small way for her patience and time.

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List of Acronyms

ANCA	Australian Nature Conservation Agency
CSR	Competitor - Stress - Ruderal
EIS	Environmental Impact Statement
ICMC	Illawarra Catchment Management Committee
LAC	Limits of acceptable change
NPWS	NSW National Parks and Wildlife Service
PERL	Pacific Estuarine Research Laboratory
Ramsar	Convention on wetlands of international importance especially as habitat for water birds (first held at Ramsar, Iran in 1971)
TCM	Total Catchment Management

Nomenclature

Nomenclature (including authors) follows Harden (1990-1993) and recent revisions accepted by the National Herbarium of NSW.

Leptospermum juniperinum

Chapter 1 General Introduction

1.1 The Research Impetus

The science of wetland ecology has seen accelerating worldwide growth over the last 20 years, largely fuelled by the imperative to redress wetland loss or to counter exploitation pressure (Jacobs & Brock 1993; Mitch & Gosselink 1993; Goodwin 1994; Williams 1994). For the purposes of conservation there has been an impetus to catalogue remaining wetlands and to describe flora, fauna and communities (see Barson & Williams 1991; Pressey & Bedward 1991; Jacobs & Brock 1993; Johnston & Barson 1993 for an Australian perspective). To provide for wetland creation and restoration there has been a need to understand wetland function, dynamics and the ecology of wetland plants (e.g. Hammer 1992; Mitch & Gosselink 1993; Zedler 1996).

In NSW, Australia, ninety percent of all coastal wetlands are found north of Sydney (Adam *et al.* 1985; Pressey & Harris 1988). Thus scientific focus and protection have centered on the extensive dunal wetlands of the Central and North Coast (Pressey & Harris 1988; Timms 1988; Jacobs & Brock 1993). South coast freshwater wetlands have remained virtually unstudied. Yet their relative rarity enhances their worth; as habitat for fauna, as drought refuge for migratory and nomadic birds, and as sites harbouring rare species.

This paucity of knowledge has contributed to wetland loss or degradation on the south coast. With the possible exception of the Jervis Bay area (Department of Planning 1992; 1995; Cho *et al.* 1995), the envisaged economic values of infilling, draining or modifying south coast wetlands have never been countered by a recognition of detrimental consequences. European settlement was from earliest times concentrated on the fertile alluvial margins of rivers (Bayley 1975; Antill 1982). In more recent times, urban and tourist developments have fringed many estuaries, bays and lakes. Acid soils, erosion, river entrance sedimentation, loss of fish stocks, reduction in water quality and loss of biodiversity are some of the results largely unforeseen.

Even today, wetland attributes are often only recognized in the context of an impact statement, which may be overridden by the pressure of development (Department of Planning 1987, 1990; Boyd 1988; Winning 1990; Adam 1992, 1995; Illawarra Catchment Management Committee 1993; Bowen *et al.* 1995). Secondary wetlands (i.e. unlisted in Adam *et al.* 1985 or Australian Nature Conservation Agency - ANCA 1996) are particularly susceptible. Much damage to wetland margins and infilling of ephemeral and smaller permanent water bodies occurs outside legislative control and is often not reported in the local media (Fig. 1.1).

In this thesis I present the results of research centered on Coomonderry Swamp, the largest freshwater, coastal wetland in the NSW southern region (Figs. 1.2 & 1.3). The work begins with the primary requirement of description, focussing on the flora and plant communities. Comparisons are then made with a diversity of other local wetlands in order to assess the value of Coomonderry Swamp as a reference site for conservation and restoration, to analyse those broad characteristics of the environment responsible for determining floristics in coastal wetlands of the region, and to assess the distribution and abundance of key indigenous plant species over a range of wetland conditions. These sites all fall within the definitions of wetlands considered to be most relevant to this project i.e. ANCA (1996) and Department of Land and Water Conservation (1996) (Appendix 1).

A

B

Figure 1.1 A - Wetland No. 376 (Adam *et al.* 1985) at Shellharbour, a proposed marina development. B - A construction site at Berkeley, south of Wollongong, NSW, previously a small freshwater wetland connected with Lake Illawarra.

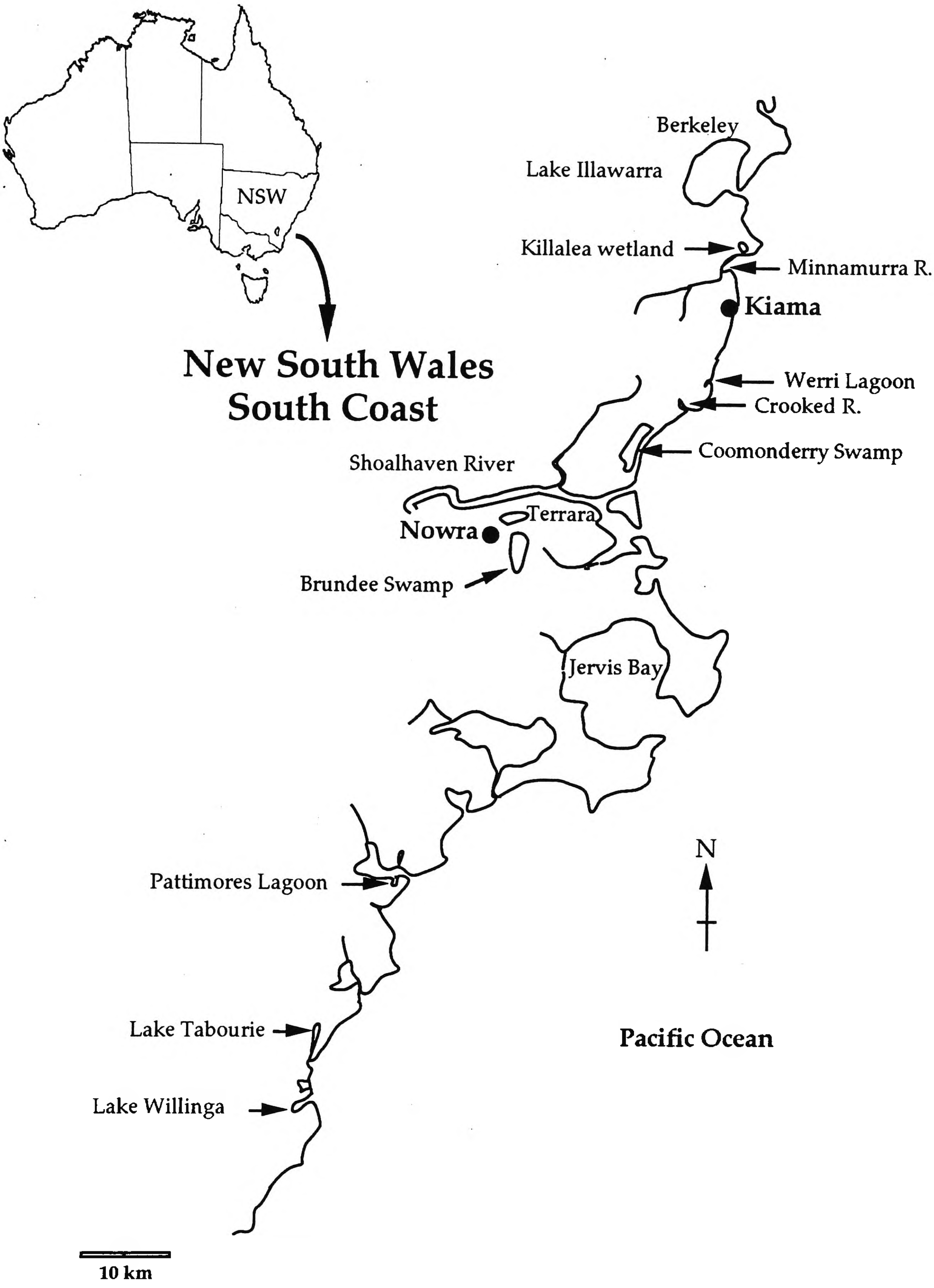


Figure 1.2 Locations of wetlands surveyed and other coastal wetlands referred to in the text.

Figure 1.3 Coomonderry Swamp looking north from the foothills of Coolangatta Mountain. Agricultural land, including turf farms, abuts the western and southern wetland margins. Areas of wet meadow (far right) and open water are more prevalent in the southern and northern parts. Sedgeland fills the central body of the wetland. A sedgeland - swamp mahogany - open-forest transition borders the entire eastern margin.

The study proceeds to an examination of function with data collected on spatial and temporal vegetation dynamics at Coomonderry Swamp. The spatial integrity of zonations is examined and a model of cyclic change is applied to the temporal data set. Plant interactions along the elevation gradient are also considered and the utilization of plant species, or suites of species, as indicators of boundaries is evaluated.

The final component explores the ecology of five dominant woody plant species of Coomonderry Swamp. An experimental approach was designed which would allow the outcomes to be applied to restoration projects. Temporal monitoring of cleared plots within wetland vegetation provided the opportunity to collect data on spatial dynamics, and disturbance and seasonal effects on weed versus indigenous plant invasion, providing an invaluable adjunct to the earlier study of vegetation dynamics.

1.2 Wetlands of the NSW South Coast

In the Sydney region, few wetlands remain undamaged or entirely protected. For example, the catchment of the substantial estuarine system of the Georges River and Botany Bay is largely urbanized or industrialized (Robinson *et al.* 1988). Mangrove and saltmarsh regions proximately protected under RAMSAR and as National Park (i.e. Towra Point Nature Reserve) are ultimately dependent on the maintenance of whole catchment water quality. Mitchell and Adam (1989a & b) have recorded changes in vegetation at Towra Point (and of major concern, a decline in saltmarsh) which relate to historical patterns of usage and to increased nutrient runoff and sediment accretion. Freshwater wetlands are poorly represented in the Sydney area and often contain significant numbers of introduced taxa (Benson & Howell 1994).

Immediately south of Sydney, the coastal strip narrows where the mountain range abuts the coastline. Upland swamps of these ranges are on poor farming soils and have been protected within water catchment areas. They are of extreme scientific interest and some have been well studied (Kodela & Hope 1992; Keith & Myerscough 1993; Keith 1994; Stricker & Wall 1995; Kodela *et al.* 1996). The next coastal wetlands of any significance border Lake Illawarra and its tributaries. Here again, urban and industrial development are intense and wetland protection and rehabilitation have followed a long period of neglect. Since the 1970's, authorities have been instituted to supervise and manage the hydrology and ecology of this waterway and a number of studies and reports have resulted (e.g. Mills 1983, 1985; Yassini & Clarke 1985; Yassini 1985; King 1988; Chafer 1991; Chenhall *et al.* 1994; Ohmsen *et al.* 1995).

Several inventories have recognized the importance of wetlands south of Lake Illawarra (Goodrick 1970; Blachford & Reeks 1976; Bell & Edwards 1980; Moss 1983; Adam *et al.* 1985; West *et al.* 1985; Lawler & Porter 1990; ANCA 1996). However only two comprehensive studies concentrating on the vegetation at specific sites have been reported in recognized scientific journals (see Adam *et al.* 1985; Pressey & Harris 1988; Lawler & Porter 1990; Jacobs and Brock 1993, Boon & Brock 1994 for review). Carne (1989) reported on the relationship between geomorphology and the distribution of mangrove and saltmarsh communities of the Minnumurra River and Clarke (1993) presented a detailed interpretation of community structure on the margins of Jervis Bay. Numerous unpublished reports have accompanied the protracted debate on land use adjoining Jervis Bay. Recognition and documentation (Cho *et al.* 1995) of the unique natural values of the bay and its surrounds have finally resulted in increased areas of protection (Department of Planning 1992; 1995) (Fig. 1.4). Further south, much of the natural vegetation along the numerous small lakes, lagoons and estuaries remains relatively unspoiled, however there has been little dissemination of information beyond the municipal level regarding the extent of wetland degradation or loss (pers. obs.). Evaluation beyond superficial inventory is urgently needed for the wetlands of the far south coast of NSW, although, in keeping with the NSW Government Estuary Management Policy, management plans for estuaries have been adopted, or should be in preparation (e.g. Shoalhaven City Council 1995, 1996a,b & c).

1.3 Reference Sites for Wetland Conservation and Restoration

In Australia wetland conservation has historically been hampered by a lack of uniformity between the States and by conflict, or lack of communication between the plethora of authorities responsible for wetland management within each State (Barson & Williams 1991; Donohue & Phillips 1991; NSW Government 1992). In NSW there has been an attempt to coordinate the activities of government, conservation bodies and the community through the unifying, 'bottom up' process of Total Catchment Management (TCM, Catchment Management Act 1989) (Department of Planning 1990; NSW Government 1992, 1994; Department of Land & Water Conservation 1996).

As well, methodologies have been suggested for the process of planning for wetland conservation which are designed to derive baseline abiotic and biotic data for high value wetlands. For example the 'Limits of Acceptable Change' (LAC) approach has been considered highly appropriate for application to wetlands in NSW (Department of Water Resources 1990; Claridge 1991; Shaw 1991; ICMC 1993). The central tenet of LAC is to implement management such that changes in condition of the wetland

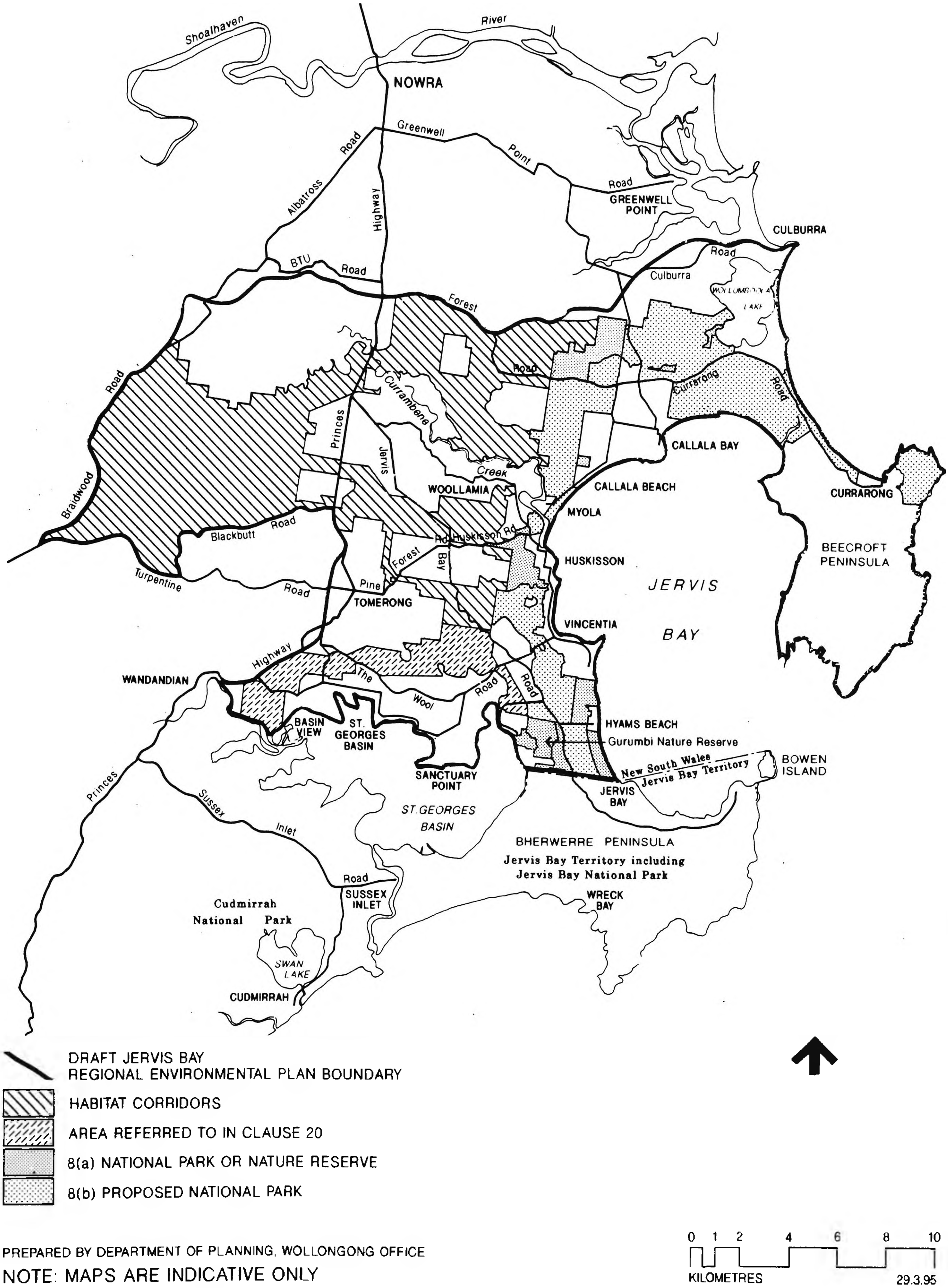


Figure 1.4 Jervis Bay habitat corridors and National Park (Department of Planning 1995, reproduced with permission).

fluctuate within acceptable ranges. While wetlands are beginning to be managed in a way that resembles the LAC approach (for example Spring Creek, Kiama and Lake Illawarra), a set of uniform guidelines and suitable indicators for the procedure is yet to be agreed on (Claridge 1991). Perhaps the greatest difficulty with the LAC approach is determining the range of acceptable change for indicators without being able to evaluate wetland responses to extreme events via long term monitoring. In many instances wetlands planning procedures need to be in place irrespective of whether or not they are supported by sufficient survey.

The 'reference system' concept has much in common with the LAC approach since it also requires the collection of base line data for a range of important attributes. Such data may be used for resource management, restoration planning and to evaluate the functional equivalency of restored sites (Zedler *et al.* 1992). The Pacific Estuarine Research Laboratory (PERL) (1990) employed the 'reference data set' concept throughout their manual for assessment of restored and natural wetlands in southern California. They noted the difficulties of characterizing reference models where most wetlands had been disturbed, spatial heterogeneity within and between wetlands was great, and only long-term monitoring could account for the impacts of extreme events. PERL (1990) concluded that optimally, a range of wetlands needed to be studied over a long term (i.e. 20 years) to provide adequate models for comparison. Hobbs and Norton (1996) have also emphasized the problems of identifying 'static and predictable' 'natural' systems as reference sites. They pointed out that the term 'natural' was ambiguous, that all systems were dynamic, and that historical conditions of 'naturalness' were often unattainable. Hobbs and Norton (1996) concluded that reference systems were useful as a guide to restoration planning when based on similar landform, soil, biotic, and climatic conditions; but could apply unnecessary constraints and hence be unobtainable as a goal.

In Australia generally, and on the south coast of NSW in particular, the extent of site degradation has not progressed to that of the southern Californian coast, and high value wetlands able to serve as reference sites are more easily identifiable. For example, Clarke (1993) applied the term 'reference system' to Jervis Bay in order to stress this site's appropriateness for providing baseline data on saltmarsh and mangrove communities against which future changes could be measured and other areas compared.

1.4 Coomonderry Swamp - a potential reference site

The relative rarity of freshwater wetlands on the south coast of NSW, makes the evaluation and monitoring of remaining unspoiled examples critical. This is particularly so considering the large number of freshwater creation and restoration programs being undertaken or envisaged for the region. Coomonderry Swamp (Figs. 1.2 & 1.3) has for some time been recognized as a wetland of primary significance because of its size and state of preservation (e.g. Goodrick 1970; Briggs 1975, Moss 1983, Adam *et al.* 1990; Lawler & Porter 1990; Kevin Mills & Associates 1993) although its value has failed to be recognized by some key planning authorities (Department of Planning 1993). It is remarkable, given the degree of wetland loss on the Shoalhaven River floodplain that Coomonderry Swamp should still retain large tracts of unspoiled vegetation (Appendix 2). The wetland supports a high diversity of wetland plants in a variety of wetland habitats and these in turn provide the food, shelter and refuge for a large number of fauna.

Approximately one third of Coomonderry Swamp is protected within Seven Mile Beach National Park and the wetland has been listed on the National Trust of Australia (NSW) (de Jong & Kodela 1995) and as an important wetland (ANCA 1996). The NSW National Parks & Wildlife Service (NPWS), while encouraging research in this system (e.g. Murphy 1994; Daly 1995) admit the resource constraints limiting their own programs for study (NSW NPWS 1996). A number of surveys have dealt with the avifauna. Coomonderry Swamp is known to support a diversity of waterbirds, including large populations of Eastern Swamp Hen (*Porphyrio porphyrio)* and Coot (*Fulica atra*), and smaller populations of Black Duck (*Anas superciliosa*), White-eyed Duck (*Aythya australis*), Musk Duck (*Biziura lobata*), Hoary-headed Grebe (*Podiceps poliocephalus*) and Black Swan (*Cygnus atratus*). The area is known for a number of rare bird sightings including the Australasian Bittern (*Botaurus poiciloptilus*) and Jabiru (*Xenorhynchus asiaticus*). In just a single six hour survey, 39 bird species were recorded in 11 bird habitats (Lawler & Porter 1990) which represented the greatest diversity of avifauna observed in their Nowra district survey. Mitchell McCotter & Associates Pty Ltd (1991) compiled, from a variety of sources, a list of 117 native bird species, while a preliminary faunal list prepared by the Shoalhaven Conservation Society, the Shoalhaven Birdwatcher's Group and National Parks and Wildlife Service contained 98 native bird species.

Prior to the present study the only 'in the field' inventories of plant species had been carried out by consultants on behalf of Shoalhaven City Council with respect to rezoning of land above the western margin of the swamp (Mitchell McCotter & Associates Pty Ltd 1991), and by Lawler & Porter (1990) whose description of plant habitats was ancillary to their bird surveys. Lawler & Porter (1990) established that six out of nine categories of freshwater wetland (defined by Goodrick 1970) are represented at Coomonderry Swamp. Three of these - fresh meadow, seasonal fresh swamp and open fresh water - have been considered to be of high value to birds

(Blachford & Reeks 1976). Mitchell McCotter & Associates Pty Ltd (1991) listed 164 plant species within a 2057 hectare area which included coastal plant communities to the east, and Redgum-Turpentine communities to the north and west of the wetland. Their compilation of the wetland macrophyte vegetation was not extensive.

The aforegoing discussion indicates that Coomonderry Swamp has substantial recognized ecological worth, particularly in a regional context, but that this value has remained largely unsupported by an appropriate level of research. There is a clear need for thorough description and classification of plant communities, to understand the process of vegetation change and to assess the value of Coomonderry Swamp in the context of other wetlands in the region. The present study, concentrating on the vegetation, will need to be supported by further research into the hydrology, water quality, soils and biota at Coomonderry Swamp.

1.5 Plant Community Description

The 'community' remains the most commonly used grouping unit in the description of vegetation. Important examples in the literature relevant to this study include Myerscough & Carolin (1986); Adam *et al.* (1988); Clarke (1993); Keith & Myerscough (1993); Benson & Howell (1994) and Keith (1994). Many of these researchers acknowledged difficulties with the term 'community' and included in their reports an operational definition appropriate to the context of their work. Thus in this research the term 'community' is used and, for reasons of uniformity and simplicity, the more complex phytosociological classification, using the syntaxa: class, order, alliance, association etc (e.g. Pignatti & Pignatti 1994; Pignatti *et al.* 1995), is avoided.

The term 'community' is applied to vegetation assemblages in the sense described by Austin (1991) i.e. "relatively homogeneous units within a continuum" (Fig. 1.5). Austin's (1991) definition is a functional compromise between the extremes in the continuum/discontinuum debate, however there is a need for an objective technique for defining the 'boundaries' of communities at an appropriate scale. This requirement lends itself well to the type of computerized pattern analysis which is now incorporated in most studies of vegetation distribution and community description. This is because relatively homogeneous units (e.g. quadrats in an area, or along a transect) can be identified using association analysis (e.g. based on plant species compositional similarity) and grouped together using an appropriate clustering strategy. Dendrograms and two-way tables enable the groupings (often termed communities) to be simply displayed and easily comprehended. Using an ordination technique, hypotheses can be generated regarding the causes for patterns of vegetation described and these may be evaluated by correlation if the relevant field data is able to be collected. In this study the computer package PATN (Belbin 1987) has been used in the spatial and temporal definition of community units at Coomonderry Swamp and at other wetlands (Ch. 2). The steps in the procedure using PATN, from vegetation data collection, through classification, to interpretation using environmental data, have been briefly described by Belbin (1991).

1.6 Wetland vegetation dynamics

Wetlands, particularly those dominated by short-lived plant species, are highly dynamic systems (e.g. van der Valk 1981; Keddy & Reznicek 1984; Taylor & Dunlop 1985; Onuf & Zedler 1988; Yen & Myerscough 1989a & b;

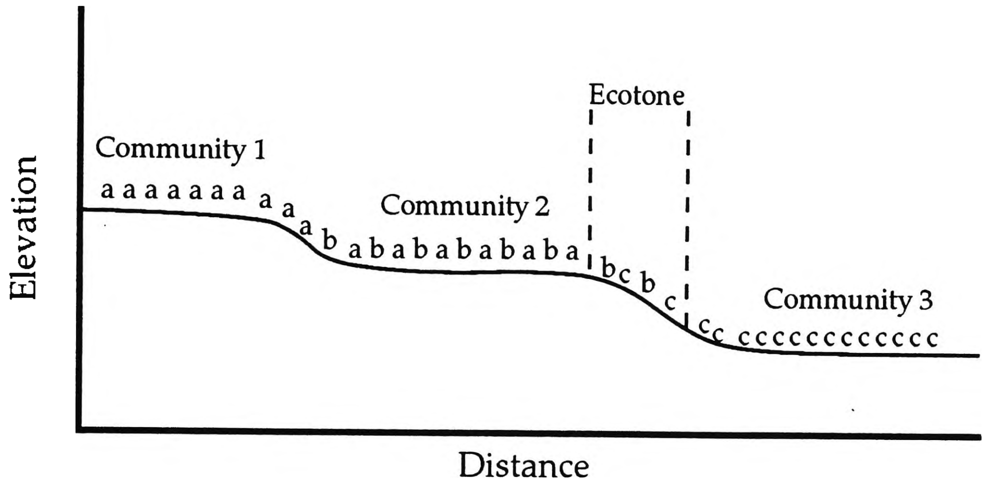


Figure 1.5 Communities as relatively homogeneous units within a continuum (adapted from Austin 1991, after Austin & Smith 1989). Represents environmental and spatial distributions of species 'a - c'.

Mesléard *et al.* 1991; Zedler *et al.* 1992; Pignatti & Pignatti 1994; Trémolières *et al.* 1994; van Groenendael *et al.* 1996). For full reference site evaluation long-term studies are desirable (Section 1.3), but the exigencies of most environmental reports and programs for protection often preclude these. However studies which are of sufficient duration to quantify at least some dynamics in species and species traits along gradients in wetlands (e.g. elevation, exposure, nutrients, species interactions) offer much greater predictive opportunities than simple inventories or descriptions.

At the system level such studies have allowed modelling of community change, both cyclic and successional, in response to inundation regime. Examples include: (i) the qualitative model of van der Valk (1981), which was founded primarily on 3 yr of study of cyclic vegetation response in prairie glacial marshes described in van der Valk and Davis (1978); (ii) the quantitative 'environmental sieve' model of Weiher and Keddy (1995a) which was based on an experimental planting and applied to a study of herbaceous riverine communities described by Day *et al.* (1988); (iii) the quantitative 'spatial computer simulation model' of Ellison and Bedford (1995) which was tested against 7 yr of vegetation data from a sedge meadow community undergoing sustained human-initiated inundation and (iv) the spatial simulation model of Poiani and Johnson (1993) which was developed and tested against 10 yr of data from a semi-permanent prairie wetland site in North Dakota.

At the species level, short-term studies have allowed prediction of comparative success when abiotic or biotic conditions alter (often involving anthropogenic disturbances or exotic species) (e.g. Yen & Myerscough 1989a & b; Zedler *et al.* 1990; Blanch & Brock 1994; Froend & McComb 1994).

The three years available for this research allowed preliminary data to be collected on vegetation dynamics at Coomonderry Swamp. Fortunately during that time, periods of rapid fluctuation in inundation regime were experienced as well as extreme drought and sustained inundation, and a range of species compositional and structural changes were described (Ch. 3). However this work will need to be continued so that sets of conditions (with past histories) may be better replicated, the full range of alternate vegetation states experienced, and predictions and hypotheses pertaining to cyclic change and species interactions verified. Eventually long term monitoring should allow differentiation between cyclic dynamics and directional (successional) changes associated with increased human impacts on the catchment (van Groenendael *et al.* 1996).

1.7 Wetland restoration

In NSW programs of restoration, often small scale, have accompanied the relatively recent recognition of the worth of wetlands. Within the local region i.e. within 40 km of Coomonderry Swamp) there are numerous examples (Fig. 1.6): Spring Ck. and Jerrara Dam, Kiama; Frog's Hollow, Bomaderry; Rocklow Ck., Minnamurra; and Killalea Nature Reserve, Shellharbour. Most involve revegetation with only minor alterations to hydrology. There are also local examples of wetland creation for other purposes: rehabilitation of sand mining proposed for Foy's Swamp; sedimentation trapping on streams entering Lake Illawarra and urban runoff entering Werri Lagoon; and wetland compensation proposed for development of Shellharbour wetland into a marina (Fig. 1.6). Most restoration initiatives are coordinated by local authorities, conservation groups and management bodies. 'Expert' advice is only available from private consultants, tertiary institutions, the Shortland's Wetland Centre

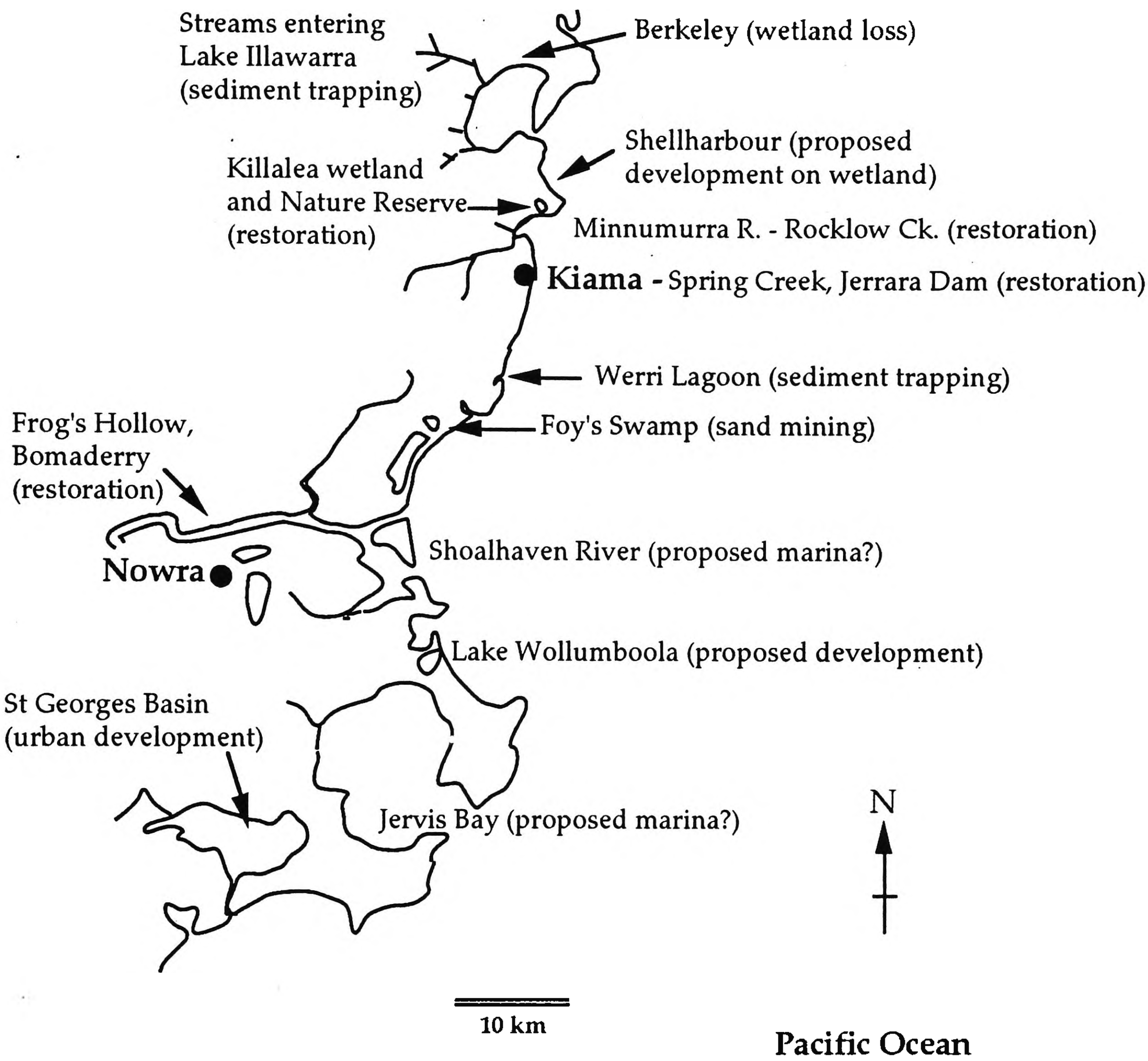


Figure 1.6 Recent examples of wetland loss and development impacts on wetlands in the Illawarra - Shoalhaven Regions. Also indicated are sites where wetland restoration and creation projects are proceeding or are planned.

(Hunter Region) and the 'grey' literature (pers. obs.). The time and financial costs can be great. For example, the adoption of a rehabilitation program for Spring Ck., Kiama followed four years of planning, numerous consultancies and a five year capital works funding of $295,900 (Council of the Municipality of Kiama, unpubl. report 1996).

"The goal of restoration is to provide self-sustaining ecosystems that closely resemble natural systems in both structure and function" (Zedler 1996). Some concensus on guiding principles to achieve this goal has developed over the short history of wetland restoration in the USA (e.g. Mitch & Gosselink 1993; Barnett *et al.* 1994; Williams 1994; Zedler 1996). The main principles are: (i) the need to understand wetland function in order to restore or create wetlands able to evolve naturally in the existing hydrologic landscape with minimum engineering and maintenance; (ii) the importance of incorporating a regional perspective (Section 1.3); (iii) having clear goals for the project, but which allow for flexibility and the opportunity for adaptive management; and (iv) the need for adequate monitoring and assessment so that function can be evaluated, new knowledge applied iteratively and information communicated to assist other projects.

In a more general review of the state of restoration ecology, Hobbs and Norton (1996) also noted the need for general guiding principles and the development of methodologies for restoration. They identified seven key processes, three of which (determining "realistic goals for reestablishment of species", "developing practical techniques for implementing these restoration goals at a scale commensurate with the problem" and documenting and communicating techniques) are the focus of the woody plant restoration experiment described in Chapter 4 of this report.

There has been an urgent need for wider communication of general wetland research in Australia (Boon & Brock 1994) irrespective of the more specific requirement for restoration information. The American literature on wetland creation and restoration is extensive, but is concentrated on the use of herbaceous vegetation. The use of non-woody species, most often Cyperaceae and Typhaceae, for sediment entrapment, nutrient uptake for water purification, and for mine rehabilitation has also been the emphasis in the Australian literature (e.g. Mitchell & Williams 1982; Allender 1984; Roser *et al.* 1987; Breen & Chick 1989). Published research devoted specifically to wetland restoration and concentrating, at least in part, on woody plant ecology is very sparse (Mitch & Gosselink 1993; Adam 1995). The work by Hammer (1992) is significant because it compiles a wealth of material on this subject previously hidden in the USA 'grey' literature and because it lists for individual species the tolerances to inundation and requirements for planting. Unfortunately much information on the ecology of woody wetland species is not transferable to Australian conditions.

The need to direct research towards understanding more about the ecology of indigenous woody species and their appropriateness for wetland restoration was emphasized by an examination of the local situation. All the restoration projects listed earlier have involved some planting with woody species. This is not surprising since many remaining wetlands in the region had been converted, by clearing and grazing of wooded margins, into rush and sedge swamps fringed by wet meadow. For this reason also local wetland creation projects (for compensation or mine rehabilitation) should have some requirement for the planting of indigenous woody species.

It is a major concern that development applications have a likelihood of success if Environmental Impact Statements (EIS's) incorporate plans for wetland compensation (nearby wetland creation) (Bowen *et al.* 1995). This is despite the fact that the wetland targeted for alteration may not have been well assessed (or could be restored if previously degraded) and despite little historical evidence for the success of wetland compensation (Krohle 1989; Mitchell 1992; Adam 1995; Bowen *et al.* 1995; Zedler 1996).

Several (unplanned) lines of investigation evolved during the experimental restoration work. Results for two of these peripheral studies are presented in Chapter 4. They serve to emphasize a central tenet of restoration (Jordan *et al.* 1987) i.e. accumulating ecological data is an unavoidable benefit of carrying out restoration.

1.8 Aims of the Study

1.8.1 General Aims

In a region where there has been little investigation of the vegetation ecology of wetlands, the obvious question was: where to begin? What research direction(s) would have some immediate value in conserving local wetlands, while providing a platform for future investigation? A review of the literature identified three broad facets of wetland science in each of which it was considered that a research direction with substantial benefits could be followed. These were:

- the description of wetland biota and structure.
- the understanding of wetland function.
- the restoration and creation of wetlands.

Deciding on Coomonderry Swamp as the primary site for centering the research was a much simpler decision given its size, relatively unspoiled condition and obvious regional significance. The general aims of the study arising from these decisions were: (i) to describe the vegetation and plant community structure at Coomonderry Swamp; (ii) to examine the vegetation dynamics at Coomonderry Swamp; and (iii) to investigate methods for using the dominant woody species occurring at Coomonderry Swamp for restoration at nearby degraded sites.

1.8.2 Specific Aims

Chapter 2 An analysis of plant communities at Coomonderry Swamp with comparisons to other wetlands on the south coast of New South Wales.

(i) to provide a detailed survey of the plant species composition, distribution, abundance and structure at Coomonderry Swamp.

(ii) to give a first account of the floristics at a range of other south coast wetlands

(iii) to compare community types, species richness, and distribution and abundance of key species among local coastal wetlands.

Chapter 3 Vegetation dynamics at Coomonderry Swamp.

(i) to determine if plant species changes along the elevation gradient vary spatially within structurally similar units of disturbed and undisturbed vegetation.

(ii) to identify broad scale changes and long term anthropogenic impacts on Coomonderry Swamp and its catchment.

(iii) to determine if plant communities change through time. How substantial are temporal variations in community attributes (i.e. plant species abundance and distribution, plant species richness)?

Intensive study of the wet meadow transition (i.e. Transect 1 wet meadow to open water/dry mud):

(iv) to investigate the potential abiotic causes for observed vegetation dynamics at the community level and at the species level.

(v) to apply a model of cyclic vegetation change in wetlands to the data set. Are the dynamics of herbaceous vegetation able to be predicted?

(vi) to examine plant interspecific covariances. Do they vary through time? Do they vary in response to the transition along the gradient from mesic to harsh conditions?

Chapter 4 Ecological implications of a woody plant restoration experiment.

(i) to investigate the relative establishment success of seeds and tubestock from five indigenous woody species following planting in previously cleared and grazed wet meadow.

Additional studies arising:

(ii) to examine spatial variation in vegetation within wet meadow (a supplementary investigation to Section 3.2).

(iii) to investigate the relationship between surrounding vegetation and invasion of gaps by stoloniferous and rhizomatous species.

(iv) to investigate inundation regime and seasonal influences on weed vs indigenous invasion of gaps in wet meadow.

Melaleuca linariifolia

Chapter 2 An analysis of plant communities at Coomonderry Swamp with comparisons to other wetlands on the south coast of New South Wales.

2.1 Introduction

The description of pattern is a primary requirement of ecology. For a system, such as Coomonderry Swamp, which has recognized values and attributes related to its location, size, state of preservation and geographic isolation (Section 1.4), such work is imperative, given the potential for future damage to its catchment.

In this chapter I firstly address the need for a comprehensive description of the flora and plant communities at Coomonderry Swamp. The communities are then assessed in a broader context. Comparisons are made with eight other local wetlands which differ markedly in disturbance regime and geomorphology and also with wetlands described in some other published reports. These include studies of a range of wetland associated communities at Jervis Bay (Clarke 1993; Mills 1995), estuarine communities at Minnamurra River (Carne 1989), foreshore vegetation of Lake Illawarra (Yassini & Clarke 1985; Yassini 1985), and upland swamp plant assemblages (Kodela & Hope 1992; Keith & Myerscough 1993; Stricker & Wall 1995; Kodela *et al.* 1996). Relationships are also examined between wetland environments of the Sydney region (Benson & Howell 1994) and with similar coastal environments of the central coast of NSW (Myerscough & Carolin 1986).

Comparisons were made with other wetlands to allow: (i) better insight into the relationship between distributions of communities (or species) and environmental factors (c.f. Grime *et al.* 1988); (ii) better determination of the distributions of species which may be poorly known e.g. those belonging to the Juncaceae, Cyperaceae and Poaceae (Adam 1981b; Adam *et al.* 1988; Clarke 1993; Johnson 1993); and (iii) better evaluation of Coomonderry Swamp as a reference site.

In response to the need to work towards a broader framework of community classification of wetlands in NSW (Adam *et al.* 1988), the terminologies suggested by Adam *et al.* (1988) and Zedler *et al.* (1995) for saltmarsh and adjoining communities; by Myerscough and Carolin (1986) for coastal sand and associated wetland communities; and by Goodrick (1970) for wetlands in general, are used, or at least referred to, where vegetation units are considered to be comparable.

Some communities described emphasise the dynamic nature of wetlands and the requirement for at least some temporal evaluation of vegetation. For example open water and ephemeral communities may occupy the same space, with their alternation being dependent on the particular regime of conditions. In this chapter, clustering and ordination techniques were used to correlate floristic patterns to environmental variables on the broader scale of differences found within and among the variety of wetlands surveyed. Hypotheses concerning the causes of finer scale temporal and spatial changes of vegetation within Coomonderry Swamp are further considered in Chapters 3 and 4.

This report does not provide an exhaustive list of all community types found in the region. Many wetlands in the area cited in inventories (Adam *et al.* 1985; West *et al.* 1985; Cho *et al.* 1995; ANCA 1996), await ecological investigation, and to these must be added numerous ephemeral wetlands and periodically wet environments which have not been mapped or recorded. Omitted from the present study are examples of coastal wet heaths (coastal bogs, Goodrick 1970) which are located on the margins of Jervis Bay. Analogous communities on the central coast of NSW have been described by Myerscough and Carolin (1986). A number of saltmarsh assemblages known to occur in the region (see Adam *et al.* 1988; Clark 1993) are also not included. In addition, time constraints precluded examination of the few, other south coast dunal systems (Timms 1988; Norris & Maher 1995).

2.2 Plant communities at Coomonderry Swamp

2.2.1 Aim

To provide a detailed survey of the plant species composition, distribution, abundance and structure at Coomonderry Swamp.

2.2.2 Methods

2.2.2.1 *Site characteristics*

Coomonderry Swamp (Table 2.1) is equidistant between the large south coastal towns of Kiama and Nowra (Fig. 1.2) and has a catchment of 1530 hectares. It covers approximately 670 hectares, filling a depression stretching for more than five kilometres adjacent to the open-forest vegetation of Seven Mile Beach National Park (Figs. 1.3, 2.1). Coomonderry is a last vestige of once extensive areas of wetland associated with the Shoalhaven River and Broughton Creek (Appendix 2). Almost all of these swamps were drained at various times for grazing purposes with consequent acid-soil problems recently becoming apparent (DoL & WC 1995; Flewin 1996). Immediately to the north of Coomonderry Swamp, a portion of what was once Foy's Swamp (Fig. 3.9) is now a sand mine (Fig. 1.6).

Coomonderry Swamp is a dune-contact wetland (B. Timms pers. comm.) although the term 'lake', usually employed in the typology of dunal

Table 2.1 Characteristics of wetland sites and extent of vegetation study.

Site	Size (km^2)	Geomorphology	Disturbance history	Survey
Killalea Swamp (375) (SB009NS) 34 34 S, 150 52E	0.2	Fresh-brackish, dunal swamp	Probably cleared. Grazed until recently. Wholly protected within State Recreation Area.	Comprehensive: 3 transects and perimeter survey (110,72,56 m)
Werri Lagoon (371a) 34 44 S, 150 50E	0.8-6.2 (17.0)	Estuarine lagoon	Cleared and grazed freehold land. Drained regularly - intermittently open.	Comprehensive: 3 transects and perimeter survey (56,50,104 m)
Crooked River 34 46S, 150 49E	0.2-0.5 (28.6)	Estuarine lagoon	Degraded forest, cleared and grazed freehold land. Silted entrance - intermittently closed.	Preliminary: 2 transects: forest to saltmarsh (80,222 m)
Coomonderry Swamp (370) (SB006NS) 34 48S, 150 44E	5.9-6.7 (15.3)	Fresh, dunal swamp	Western margin: cleared and grazed freehold land. Eastern margin relatively undisturbed.	Comprehensive: 9 transects and perimeter survey (204,210,120,130, 290,72,96,120,120 m)
Terrara Swamp 34 53S, 150 39E	1.7-2.0	Fresh, floodplain swamp	Extensively drained, fallow or grazed freehold land.	Preliminary: 1 transect in wet meadow (60 m)
Brundee Swamp (344) 34 55S, 150 39E	4.0	Fresh - brackish, floodplain swamp	Extensively drained, fallow or grazed freehold land. Some undisturbed, wooded wetland.	Preliminary: 2 transects: forest to wet meadow, dry meadow to tea-tree (110,200 m)
Pattimores Lagoon (294) 35 16S, 150 30E	0.5	Saline, dunal swamp	Largely undisturbed margin, but subject to periodic estuarine inflow via a canal.	Preliminary: 1 transect: forest to deep water (98 m)
Lake Tabourie (272) 35 27S, 150 25E	1.4 (43.0)	Estuarine lake	10-25% cleared, some revegetated. Uncleared margin in State Forest. Silted entrance.	Preliminary: 1 transect: sand dune-regrowth-deep water (144 m)
Willinga Lake (260) 35 30S, 150 23E	0.3	Estuarine lake	Increasing development on margins. Entrance intermittently closed. Some undisturbed margin.	Preliminary: 1 transect: forest to deep water (260 m)

Site: Wetland reference numbers (Adam *et al.* 1985; ANCA 1996) shown in brackets. Size: Ranges are given where maps and/or references differ. Variations indicate the arbitrary definition of wetland boundaries. Catchment size (if known) is shown in brackets. Survey: Length of transects shown in brackets in the order named (see Fig. 2.14). Sources: Bell & Edwards 1980; Moss 1983; Adam *et al.* 1985; West *et al.* 1985; Lawler & Porter 1990; Chafer & Marthick 1995).

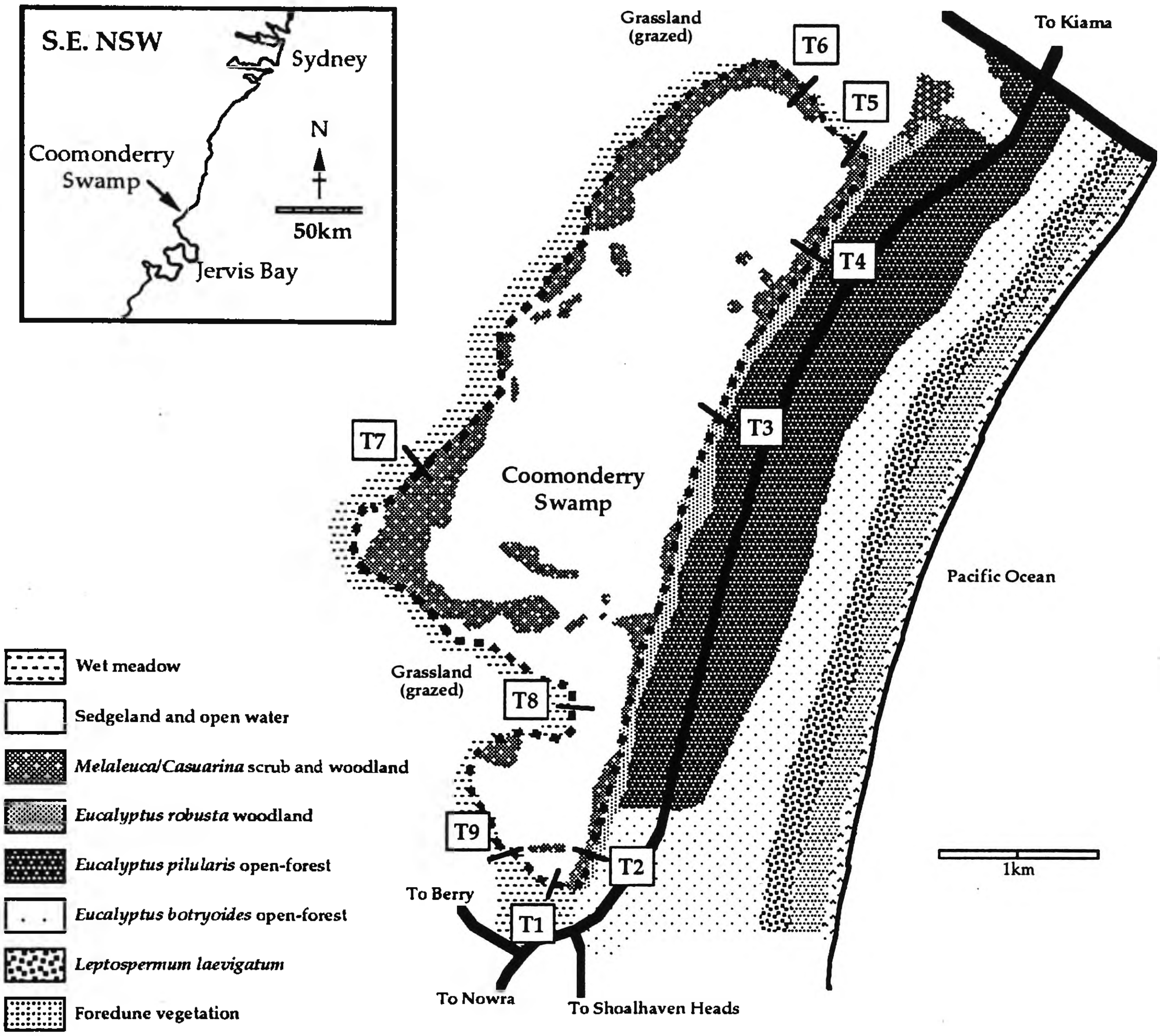
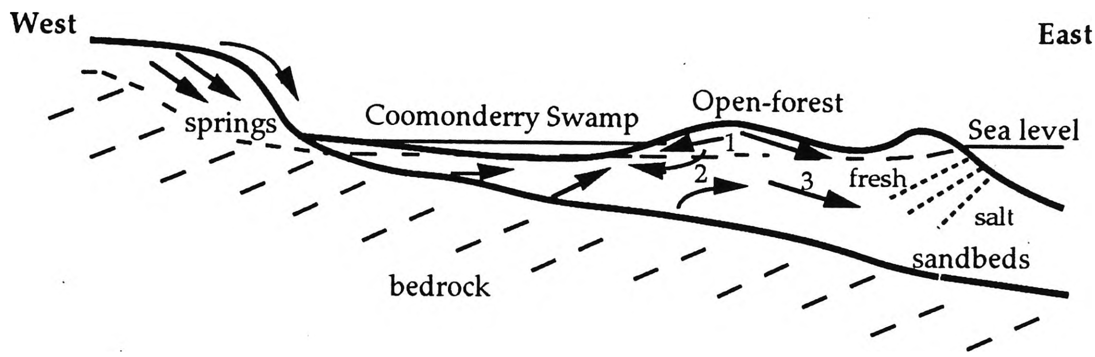


Figure 2.1 Major vegetation types and location of transects at Coomonderry Swamp and environs. Based on Mitchell McCotter & Associates Pty Ltd (1991) and de Jong & Kodela (1995).

waterbodies, can hardly be applied to Coomonderry Swamp since it is uniformly shallow (<2 m depth) and rarely supports large areas of open water. Its geomorphology (between dunes and adjacent rock) (Fig. 2.2) and chemistry (salinity usually <500 mgL^{-1}) are typical and indicative of dune-contact systems (Timms 1982, 1986, 1988). While the common indicator of dunal wetland, *Lepironia articulata* does not occur on the south coast of NSW, freshwater snails do, and these are considered to be an important component differentiating dune-contact waterbodies from other types of dune freshwater systems (Timms 1982, 1986, 1988). Indicator zooplankton have not been studied for Coomonderry Swamp.

No obvious creeks feed into Coomonderry Swamp, yet the wetland responds rapidly to rainfall events and also to periods of drought (Fig. 3.2). Inputs of water to Coomonderry Swamp are via: direct rainfall, surface run off and springs from bedrock, subsurface seepage from dune ridges, and groundwater from mounds in sand dunes and from sand-bed aquifers (Mitchell McCotter & Associates Pty Ltd 1991). Outflows occur via a southern drainage channel and by seepage into sand beds at the eastern margin.

Hazelton (1992), described the wetland soils as composed of friable organic peat (30 cm) overlying acid peats of depths greater than 100 centimetres. Below the peat, various sandy subsoils overlie Quaternary marine sands. Along the undisturbed dune-contact margin, the elevation gradient is steep (approx. 0.04 gradient) compared to much of the west and southern margins, and soils correspondingly vary from almost totally organic within the wetland to predominantly sandy on the ancient dune peaks (Fig. 2.3). Soils along the elevation gradient within wet meadow do not differ greatly (Fig. 4.4, Table 4.1) and thus variations in soil characteristics along the elevation gradient here are considered to be a function of the degree and



1. Subsurface seepage
2. Shallow groundwater flow direction
3. Regional groundwater flow direction

Water table: - - - -

Figure 2.2 Geomorphology and water flow of the Coomonderry Swamp system (after Mitchell McCotter & Associates Pty Ltd 1991).

duration of inundation. The implications for plant growth of variations in the inundation regime are considered in detail in Chapters 3 & 4.

2.2.2.2 *Survey design*

The botanical survey at Coomonderry Swamp involved investigation along nine transects which traversed all major vegetation types (Fig. 2.1, Appendix 3) supported by description of floristics in and around the wetland. Belt transects (1 m width) were situated along the elevation gradient, beginning on the landward side in visually homogeneous units of either woodland, grassland or meadow and ending in the deepest part of the wetland, often in open water or homogeneous units of deep water vegetation. Discontinuities in vegetation commonly varied in response to changes along the elevation gradient and consequently transects varied in length (Table 2.1).

Estimates of percentage cover (0, < 10%, ≥ 10%) were made for all plant species in contiguous, 2 m x 1 m quadrats along each transect. Structural characteristics of the vegetation were recorded and the following height classifications were used (after Specht 1981): (i) herbaceous layer: < 1 m, (ii) reed/sedge: 1 - 2 m, (iii) shrubland: 1 - 4 m, (iv) woodland: trees > 4 m.

Soils at *ca.* 20 m intervals along each transect were visually classified as either 'peat' (almost completely organic), 'humic' (> 50% organic but with some sand), 'sandy' (< 50% organic), 'sand' (virtually no organic material) (Fig. 2.3). Where possible, water salinity and pH were recorded at *ca.* 20 m intervals. Salinities were measured using a temperature - compensated salinity meter and pH using Universal Indicator paper or field pH meter. Elevations along transects were recorded at 2 m intervals. These were determined using an autolevel and from water depths. Elevations on all transects could be related.

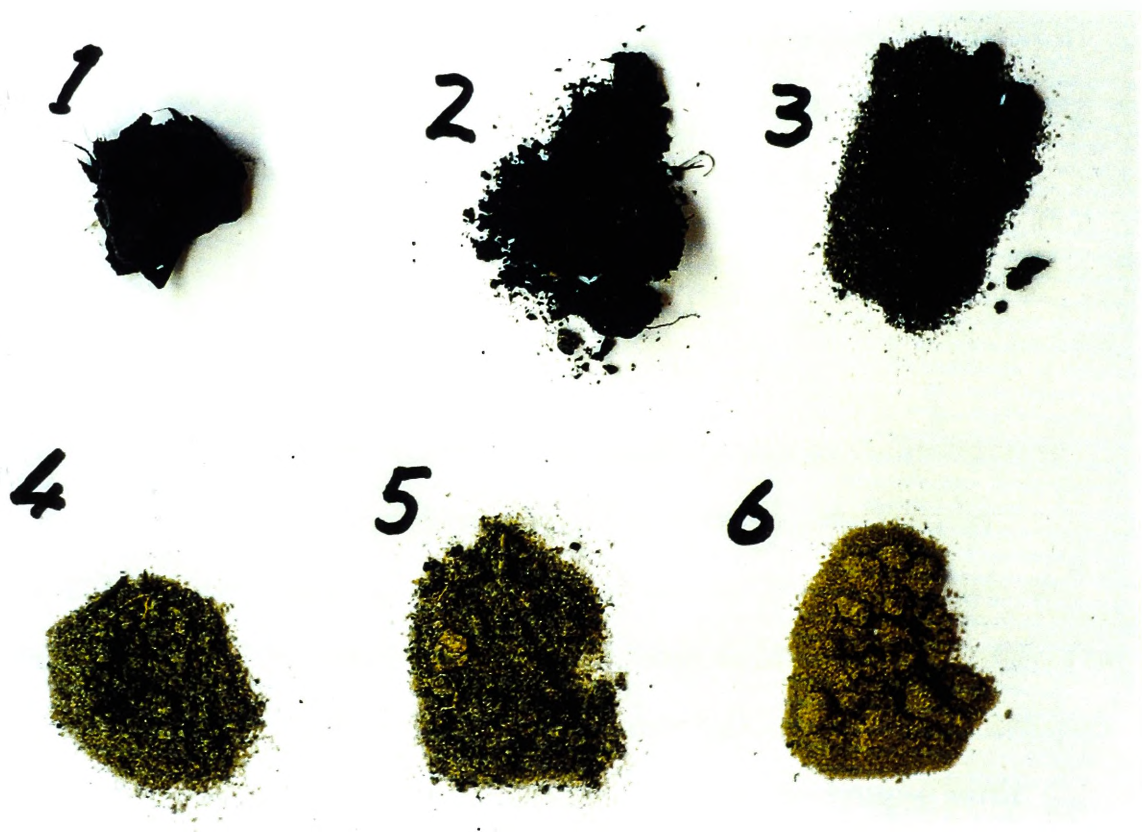


Figure 2.3 Soils along the elevation gradient of the undisturbed margin at Transect 2, Coomonderry Swamp. These soils were classified as: 1 - 'peat' (a soil from transect unit 2.3 - see Appendix 4); 2 - 'humic' (a soil from transect unit 2.2); 3 - 'humic' (a soil from transect unit 2.2, but close to the 'boundary' with transect unit 2.1); and 4 and 5 - 'sandy' (soils from transect unit 2.1). Soil 6 - 'sand' is shown for comparison. Soils classified as 'sand' were not encountered at Coomonderry Swamp.

2.2.2.3 *Transect analysis*

TWINSPAN analysis (Hill 1979; Gauch 1982) was used to cluster quadrats along each of the nine transects on the basis of plant species compositional similarity. A standard stopping rule for numbers of divisions was applied for all transects, identifying relatively homogeneous units of vegetation (termed community transect units). An example of how TWINSPAN defined these units along Transect 3 at Coomonderry Swamp is shown in Fig. 2.4 and along other transects in Appendix 4. An alternative clustering strategy used for comparison (Jaccard's coefficient with average linkage clustering) produced very similar results.

2.2.2.4 *Community analysis*

The percentage frequency of occurrence in quadrats was calculated for all species within each of the 36 community transect units identified by TWINSPAN. Cluster analysis was performed on the resulting matrix to relate the floristics of the whole wetland (cf. Keith & Myerscough 1993). The Bray-Curtis measure of dissimilarity and flexible UPGMA (unweighted pair group arithmetic averaging) agglomerative clustering technique with $\beta = -0.1$ (Belbin 1987) was chosen to analyse these data. Alternative methods again produced similar results.

Ordination using hybrid multi-dimensional scaling (HMDS) (Belbin 1987) was carried out on the Bray-Curtis association matrix derived from the initial TWINSPAN analysis of transects. Ordinations were performed in three and four dimensions with a 0.8 cut (Belbin 1987).

Following cluster analysis and ordination, hypotheses were generated regarding the relationship between floristics and soil-water characteristics, structural characteristics of the vegetation and disturbance factors. Each

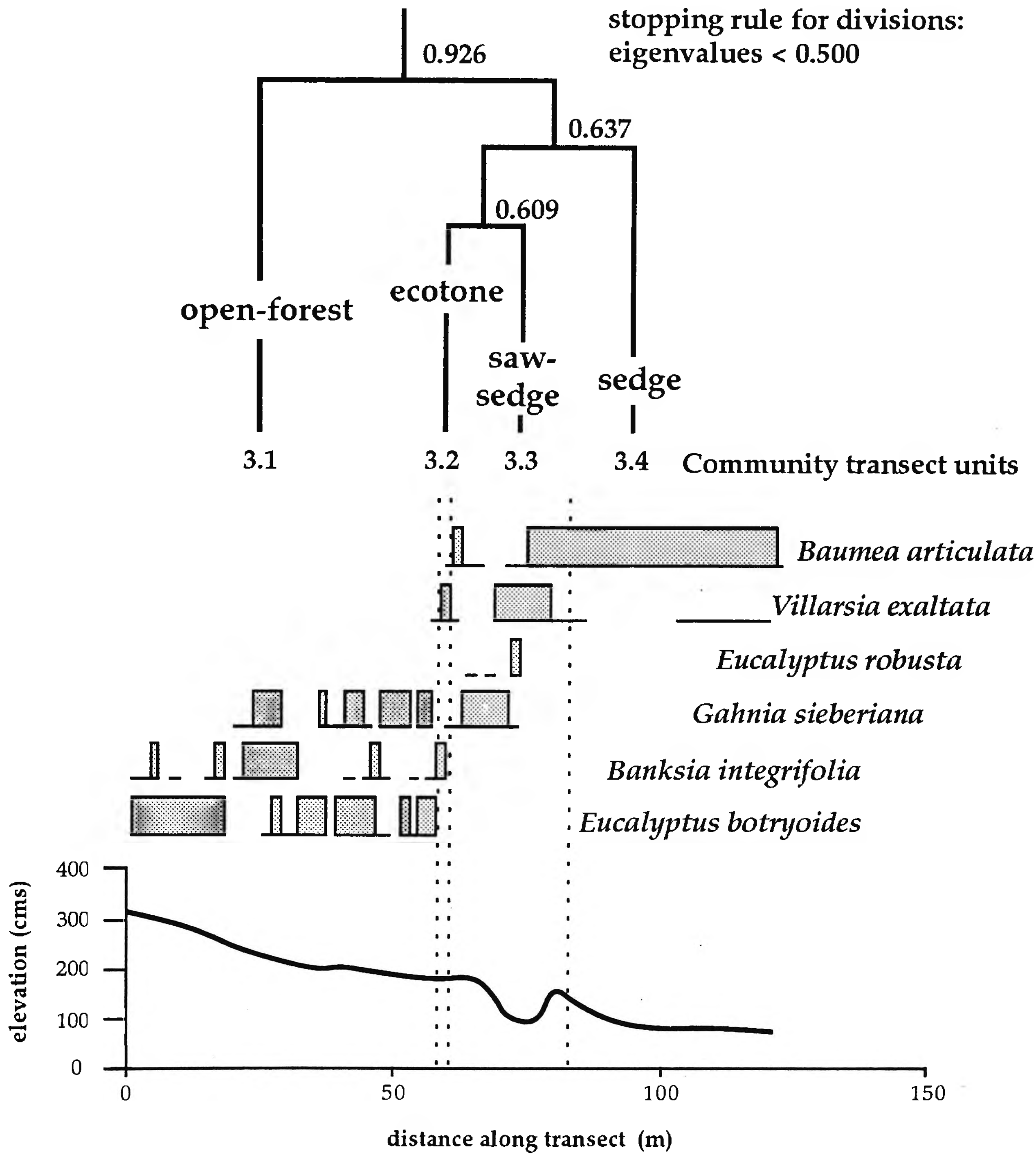


Figure 2.4 Community transect divisions derived from TWINSPAN analysis of species composition in quadrats along Transect 3 at Coomonderry Swamp. Direct gradient analysis shows the distribution and abundance of some well distributed and abundant indigenous species. Lines show presence of named species. Shaded bars show % cover ≥ ten. Transect divisions are numbered consecutively down the transect.

community transect unit was characterized by calculating values (*a posteriori*) for measures which could be indicative of each of these factors. These measures were means for: (i) relative elevation (cm); (ii) soils ranked: 1 - peat, 2 - humic, and 3 - sandy; and (iii) species richness at 10 m^2 scale (five quadrat interval). Other measures for each vegetation unit were: (i) vegetation height calculated from the formula: $[\sum(nh)]+q/[\sum n]+q$ (where 'n' = the number of quadrats with ≥ 10% cover for a given species, 'h' = ranked height class for each of these species, and 'q' is the number of quadrats having no species with ≥ 10% cover); (ii) proportion of introduced taxa and (iii) proportion of woody perennials together with longer-lived, non-woody species whose populations exhibited constancy (Putman 1994) over three years of seasonal and hydrological flux.

Pairwise correlations between each variable and each ordination vector were calculated using Pearson correlation coefficients. The significance of correlations was tested with t - tests with the level of significance reduced to $P = 0.001$ by the Bonferroni procedure to compensate for the number of correlations.

2.2.3 <u>Results</u>

2.2.3.1 *Community analysis*

Over 200 plant species were recorded within Coomonderry Swamp and along its margins (Appendix 5) and eleven communities were recognized (Fig. 2.5). For purposes of comparison with other wetlands (Section 2.3), these were further reduced to seven: with fresh wet meadow, floating mat and ephemeral meadow being considered 'local variants' of wet meadow; *Melaleuca* and *Melaleuca-Casuarina*, local variants of *Melaleuca*; and *Marsilea* and *Utricularia-Eleocharis* complexes, local variants of deep

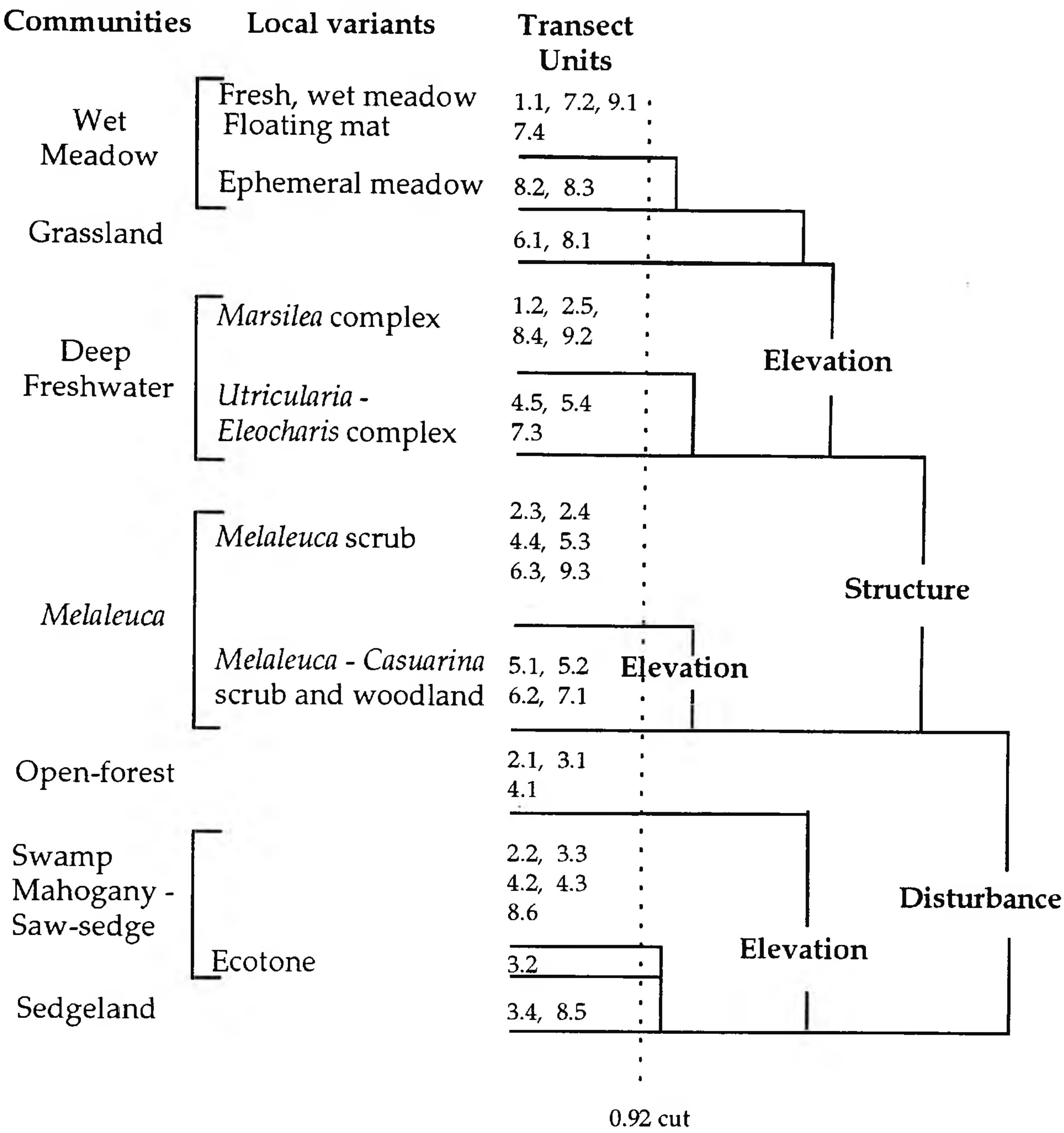


Figure 2.5 Dendrogram derived from cluster analysis of all community transect units at Coomonderry Swamp.

freshwater communities. Arrangements of communities varied little among alternative clustering procedures. Discrepancies arose in the classification of 'mixed' communities, for example, disturbed and open *Melaleuca* scrub which contained understories dominated by short-lived herb and grass species. Such units could be grouped with other *Melaleuca* communities, or alternatively, with wet meadow communities. A two-way table (Appendix 6) shows the plant species composition within community transect units and the sequencing of these units within communities derived from cluster analysis for Coomonderry Swamp and the other wetlands surveyed.

The diversity of communities found at Coomonderry Swamp reflects the complexity of factors influencing floristics. The four dimensional ordination resulted in a 24% reduction in stress (to 0.1307) over three vector analysis, and better differentiated correlated variables, albeit with a corresponding increase in 'noise' (Table 2.2). The trend in negative to positive scores for vector 1 corresponded to an increase in elevation and decrease in organic content of soils. Vector 2 correlated strongly with structural components of the vegetation, the negative to positive sequence of vector values matching a general increase in canopy height with an associated decrease in proportions of introduced taxa. Vector 3 suggested the influence of human disturbance at Coomonderry Swamp (and disturbance and stress related to inundation changes lower on the elevation gradient- Chapter 3.3). The negative to positive sequence of vector scores in this instance generally matched an increase in the proportion of introduced species and related decrease in woody perennials and longer-lived non-woody perennials. Vector 4 indicated the influence of soil characteristics with the trend from negative to positive vector scores correlated with a decrease in humic content of soil. More soil analysis is needed to define those

Table 2.2 Pearson correlation coefficients for four vector ordination of community floristics at Coomonderry Swamp with elevation, soil and variables indicative of vegetation structure and disturbance.

	Vector 1	Vector 2	Vector 3	Vector 4	Veg. height	Elev.	Introd.	Perenn.	Species rich.
Veg. height	0.049	**0.809***	-0.137	0.453					
Elev.	**0.581***	0.260	0.366	0.379	0.291				
Introd.	-0.292	**-0.640***	**0.663***	-0.177	**-0.599***	-0.057			
Perenn.	0.249	0.495	**-0.539***	0.395	0.522	0.075	**-0.721***		
Species richness	0.353	0.127	0.448	-0.084	-0.031	0.316	0.025	-0.266	
Soil index	**0.545***	0.284	0.269	**0.610***	0.386	**0.763***	-0.077	0.258	0.185

Critical value: $P = 0.001$. $^*P < 0.001$. See text for description of variables.

characteristics that influence floristics in this wetland (cf. Keith & Myerscough 1993).

The categories of factors delineated by ordination: disturbance, structure and elevation; are superimposed on the dendrogram (Fig. 2.5) to indicate their relative importance to early divisions of the cluster analysis.

2.2.3.2 *Characteristics of communities*

Five communities at Coomonderry Swamp were found along margins subject to greatest anthropogenic disturbance and consequently high proportions of ruderal species predominated.

Fresh, wet meadow (Fig. 2.6) Areas of wet meadow occurred principally on the southern and south-western margins of the wetland where heavier, peaty soils were subject to frequent fluctuations in the inundation regime (Ch. 3). These areas have been consistently grazed in the past and cattle still enter the wet meadow during periods of greatest draw-down. Wet meadow is one of the more species-rich community types in the wetland, with more than 90 species recorded in proximity to Transect 1 alone (Fig. 2.1). Wet meadow at Coomonderry Swamp was dominated by species of Cyperaceae, Juncaceae and Poaceae. Key species included *Hydrocotyle peduncularis, Triglochin procerum, Isolepis prolifera, Juncus polyanthemus, Pseudoraphis paradoxa, Paspalum distichum* and *Persicaria decipiens. Cotula coronopifolia* and *Triglochin striatum,* species commonly associated with saline environments, periodically occurred.

Floating mat An unusual community transect unit clustered as wet meadow was a floating mat of vegetation of ≥ 50 cm thickness within a stand of *Melaleuca ericifolia* in water > 1 m depth.

Figure 2.6 Fresh, wet meadow at Coomonderry Swamp.

Figure 2.7 Ephemeral meadow at Coomonderry Swamp.

Ephemeral Meadow (Fig. 2.7) During periods of severe draw-down, extensive blooms of ephemeral and opportunistic species soon covered mud in areas of previously open water. Dominant species along the upper margins, trampled by cattle, included *Cynodon dactylon, Hydrocotyle peduncularis, Axonopus affinus, Paspalum dilatatum* and *Trifolium repens.* At lower elevations *Centipeda minima, Hydrocotyle bonariensis, Myriophyllum simulans* and *Juncus polyanthemus* were common - the latter two species probably present prior to draw-down.

Grassland Grazed areas above much of the western, southern and northern margins of Coomonderry Swamp were predominantly covered with *Pennisetum clandestinum.* Other species were *Axonopus affinus, Trifolium repens, Cynodon dactylon, Hypochaeris radicata* and *Carex appressa.*

***Marsilea* complex** (Figs. 2.8 , 3.14d) Deep freshwater communities are the flooded counterparts of ephemeral communities. *Marsilea mutica* predominated beyond wet meadow, over the summer months, and in water generally less than 60 cm. Other key components included *Isolepis prolifera, Juncus polyanthemus, Triglochin procerum, Utricularia australis, Eleocharis sphacelata, Myriophyllum simulans, Pseudoraphis paradoxa* and *Paspalum distichum.*

***Utricularia - Eleocharis* complex** (Fig. 3.14d) Deep water areas of the swamp, not dominated by *Melaleuca* spp. or *Baumea articulata* (but often occurring with these), principally supported *Utricularia* spp. interspersed with tall clumps of *Eleocharis sphacelata* and *Typha orientalis.* Other floating species included *Nymphaea* spp., *Potamogeton* spp., and *Persicaria* spp.

Figure 2.8 *Marsilea* complex at Coomonderry Swamp.

Figure 2.9 *Melaleuca* thickets in sedgeland at Coomonderry Swamp.

The aforementioned communities illustrate the dynamics often associated with systems subjected to frequent disturbance (Section 3.3). Sedgelands, however, and the undisturbed, wooded, eastern margin have remained robust in the face of these short term environmental and seasonal fluctuations. Cluster analysis (Fig. 2.5) delineated five of these resilient communities.

***Melaleuca* scrub** (Figs. 2.9, 2.10) *Melaleuca ericifolia* is perhaps the most pervasive species in this wetland, occurring as thickets throughout the sedgeland and almost continuously along the 5 km length of the undisturbed margin. Remnant pockets on the western margin suggest extensive clearing. Co-occurring species varied depending on water depth and disturbance within each *Melaleuca* community. *Azolla filiculoides, Spirodela punctata* and *Persicaria praetermissa* were common understory species in standing water.

***Melaleuca - Casuarina* scrub and woodland** *Casuarina glauca* was a dominant or co-dominant woody species, often occurring above stands of *Melaleuca ericifolia* along the elevation gradient. *Carex appressa, Gahnia sieberiana, Entolasia marginata* and *Viola hederacea* were common understory species of grazed, dryer ground at the northern end of the wetland. *Isolepis inundata, Isolepis prolifera, Eleocharis acuta* and *Persicaria praetermissa* were common members of *Melaleuca - Casuarina* communities at slightly lower elevations. *Melaleuca linariifolia* was a secondary wooded component of some *Melaleuca* and *Melaleuca - Casuarina* communities.

Sedgeland (Fig. 2.9) The extensive central body of Coomonderry Swamp is covered by sedge, principally *Baumea articulata*, but also *Baumea arthrophylla*. Within this continuous 2 m tall stratum, *Villarsia reniformis*

Figure 2.10 *Melaleuca ericifolia* in deep water on the eastern margin of Coomonderry Swamp.

was found with some of the typically open water species previously described. Isolated stands of *Typha orientalis, Phragmites australis* and *Eleocharis sphacelata* were scattered throughout the sedgeland. *Baumea juncea* with *Villarsia exaltata* became increasingly common with more shallow inundation or on moist soil.

Swamp Mahogany - Saw-sedge (Fig. 2.11) The transition between sedgeland and forest is typified by open *Eucalyptus robusta* (Swamp Mahogany) woodland with isolated *Casuarina glauca* and *Melaleuca* spp., an often very open shrub/sedge stratum of *Gahnia sieberiana* (Saw-sedge), *Leptospermum juniperinum* and *Baumea* spp., and a dense grass/herb substratum dominated by *Hemarthria uncinata, Villarsia exaltata, Lobelia alata* and *Goodenia paniculata.*

Open-forest (Fig. 2.12) *Eucalyptus pilularis* open-forest, on sandier soils to the north, and *Eucalyptus botryoides* open-forest on more humic soils to the south, were clustered together in this analysis on the basis of a strong similarity in understory components. Open-forest is a relatively species rich community at Coomonderry Swamp. The usually dense small tree and shrub strata were composed of a broad range of species including *Glochidion ferdinandi, Elaeocarpus reticulatus, Banksia serrata, Banksia integrifolia, Breynia oblongifolia, Myoporum* spp., *Acacia* spp. and *Monotoca elliptica.* Understorey species included *Gahnia sieberiana, Entolasia* spp., *Oplismenus aemulus, Dianella caerulea, Pteridium esculentum* and *Lomandra longifolia.* Pockets of rainforest (Fig. 2.13) occurred throughout the open-forest and several species of vines (e.g. *Parsonia straminea, Smilax glyciphylla, Marsdenia rostrata* and *Cissus hypoglauca*) were a strong constituent of both rainforest and open-forest vegetation.

Figure 2.11 Swamp Mahogany - saw-sedge at Coomonderry Swamp.

Figure 2.12 Open-forest at Coomonderry Swamp.

Figure 2.13 *Glochidion ferdinandi* dominated littoral rainforest at Coomonderry Swamp.

2.2.4 Discussion

A significant ecological feature of Coomonderry Swamp is the diversity of its plant communities and the associated diversity of habitats available to avifauna (Blachford & Reeks 1976; Lawler & Porter 1990). The extent and state of preservation of the sedgeland - swamp mahogany - woodland - dunal transition is of great value since similar stands are poorly represented south of Sydney. Floating mats are an unusual occurrence (but see Hill & Webb 1982; Mitch & Gosselink 1993; Sasser *et al.* 1996).

Because Coomonderry Swamp is a geographically isolated example of a freshwater, dunal wetland, it has major importance as a refuge for some plant species such as *Eucalyptus robusta, Villarsia reniformis, Lilaeopsis polyantha,* regionally uncommon members of the Juncaceae, and uncommon ephemerals such as *Cyperus odoratus* (Appendix 5).

Plant communities at Coomonderry Swamp were differentiated at a relatively coarse level. The major plant communities defined (Fig. 2.5) have remained structurally consistent over time (i.e. at least 50 years - Fig. 3.9) despite the dynamic nature of some local variants within these (i.e. ephemeral, wet meadow and open water complexes - see Ch. 3).

The diversity of plant communities at Coomonderry Swamp appeared to be the consequence of a complex interaction of factors. Rates of change in the inundation regime, changes in soil characteristics and water status along the elevation gradient, and levels of anthropogenic disturbance varied between different margins of the wetland. In general terms, a toposequence: grassland - wet meadow - open water - sedgeland could be recognized on much of the northern, western and southern farmed margins. A 'hybrid' toposequence: grassland - (rarely Swamp Mahogany) - *Melaleuca* or

Melaleuca/Casuarina - open water - sedgeland was found where grazed land abutted steeper margins. The toposequence: open-forest (sometimes littoral rainforest) - Swamp Mahogany woodland - *Melaleuca* - sedgeland was developed on the eastern undisturbed fringe.

2.3 Comparison of Coomonderry Swamp with other wetlands surveyed

2.3.1 Aims

To give a first account of the floristics at a range of other south coast wetlands.

To compare community types, species richness, and distribution and abundance of key species among local coastal wetlands.

2.3.2 Methods

2.3.2.1 *Site characteristics*

Detailed descriptions of vegetation were completed at two additional wetlands; Killalea (the nearest other freshwater wetland to Coomonderry Swamp) and at a saline wet meadow site, Werri (Ooaree) Lagoon (Fig. 1.2). Preliminary surveys were made at another six wetlands (Fig. 1.2 & Table 2.1). Wetlands were chosen to represent the three major geomorphological divisions: estuarine, floodplain and dunal (Adam *et al.* 1985). Differences among wetlands included salinity, hydrology, soil type, size, and the nature and degree of anthropogenic disturbance (Table 2.1).

Detailed maps, locations, landform types, management objectives, land tenure, wetland size, bird habitat and conservation status of the wetlands surveyed have variously been described in inventories and other publications (Blachford & Reeks 1976; Bell & Edwards 1980; Moss 1983; Adam *et al.* 1985; West *et al.* 1985; Gibson 1989; Lawler & Porter 1990; Porter

1990; Chafer & Marthick 1995; Shoalhaven City Council 1995; ANCA 1996; Young *et al.* 1996).

2.3.2.2 *Survey design*

Survey design was the same for all wetlands (see Section 2.2.2). Terrara Swamp, a drained and grazed meadow, was the only site at which there was no obvious elevational change. Here one transect, discontinued after 60 m, was surveyed through the apparently uniform vegetation. Percentage cover, structural characteristics of the vegetation, soils, water salinity and pH were all described, or estimated, in the way previously indicated for Coomonderry Swamp. Water depths at these other sites were recorded at 2 m intervals along transects at the time of sampling and estimates were made of relative elevations above water level.

2.3.2.3 *Community analysis*

As for Coomonderry Swamp, 'community transect units' were identified along transects by using TWINSPAN. All community transect units (including those from Coomonderry Swamp) were compared by forming a % frequency occurrence matrix and then applying the clustering and ordination techniques in the way previously described. Once again correlations between vectors (three to five) and floristic and soil-water characteristics were performed. Additional variables included two soil ranks: 4 - sand and 5 - laterite, pH and salinity. Correlations were not performed for salinity and pH with community transect units above water level. The significance of correlations was tested with *t* - tests, with the level of significance reduced to $P = 0.001$ by the Bonferroni procedure, to compensate for the number of correlations performed. Soil-water and structural attributes of each community type derived from the clustering procedure were compared using single-factor ANOVA, with multiple comparison of means performed with Fisher PLSD tests. None of the appropriate transformations removed heterogeneity among variances and so ANOVAS were performed on the untransformed data.

2.3.3. Results

2.3.3.1 *Community analysis*

In addition to the 36 community transect units from Coomonderry Swamp, TWINSPAN analysis identified a further 46 from transects at other sites. Cluster analysis, based on the total 82 units x species (% frequency occurrence in quadrats) matrix, defined some communities and several local variants not encountered at Coomonderry Swamp (Fig. 2.14). These included dry meadow, saltmarsh, mangrove and deep estuarine communities. Swamp Mahogany - saw-sedge, sedgeland and wet meadow communities of the type found at Coomonderry Swamp did not occur, or were poorly represented at these other sites.

HMDS ordination in four vectors was selected as best for differentiating floristics over the broad range of wetland sites (Table 2.3), although some variables themselves were strongly correlated and were thus poorly separated in the ordination. The factors correlated significantly were: salinity (vectors 1 & 2), structural characteristics (i.e. vegetation height - vector 2), disturbance (i.e. introduced taxa and the proportion of perennial species - vector 3) and a range of components related to the elevation gradient (soil, vegetation height, pH, elevation, salinity - vector 4). Correlations should be treated with additional caution as the stress value in four dimensions was high (0.1843). However five vector ordination did not improve differentiation of variables although stress was reduced by 17% to 0.1533.

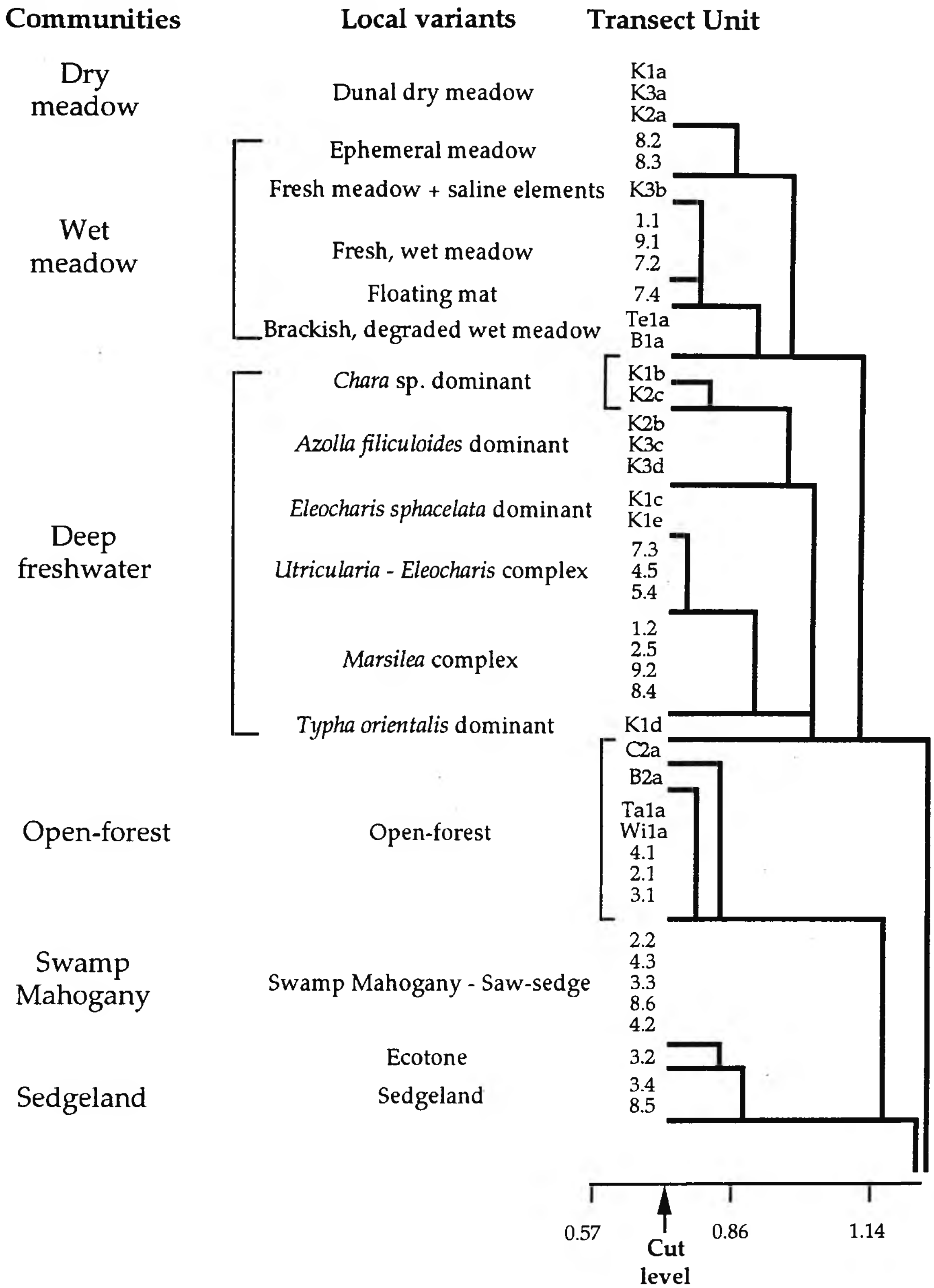


Figure 2.14 Dendrogram derived from cluster analysis of all community transect units encountered at nine South Coast wetlands. Association values are shown along the bottom. Community names for Coomonderry Swamp are abbreviated as shown in Fig. 2.4 (abbreviations for other wetlands see over page). **...cont'd**

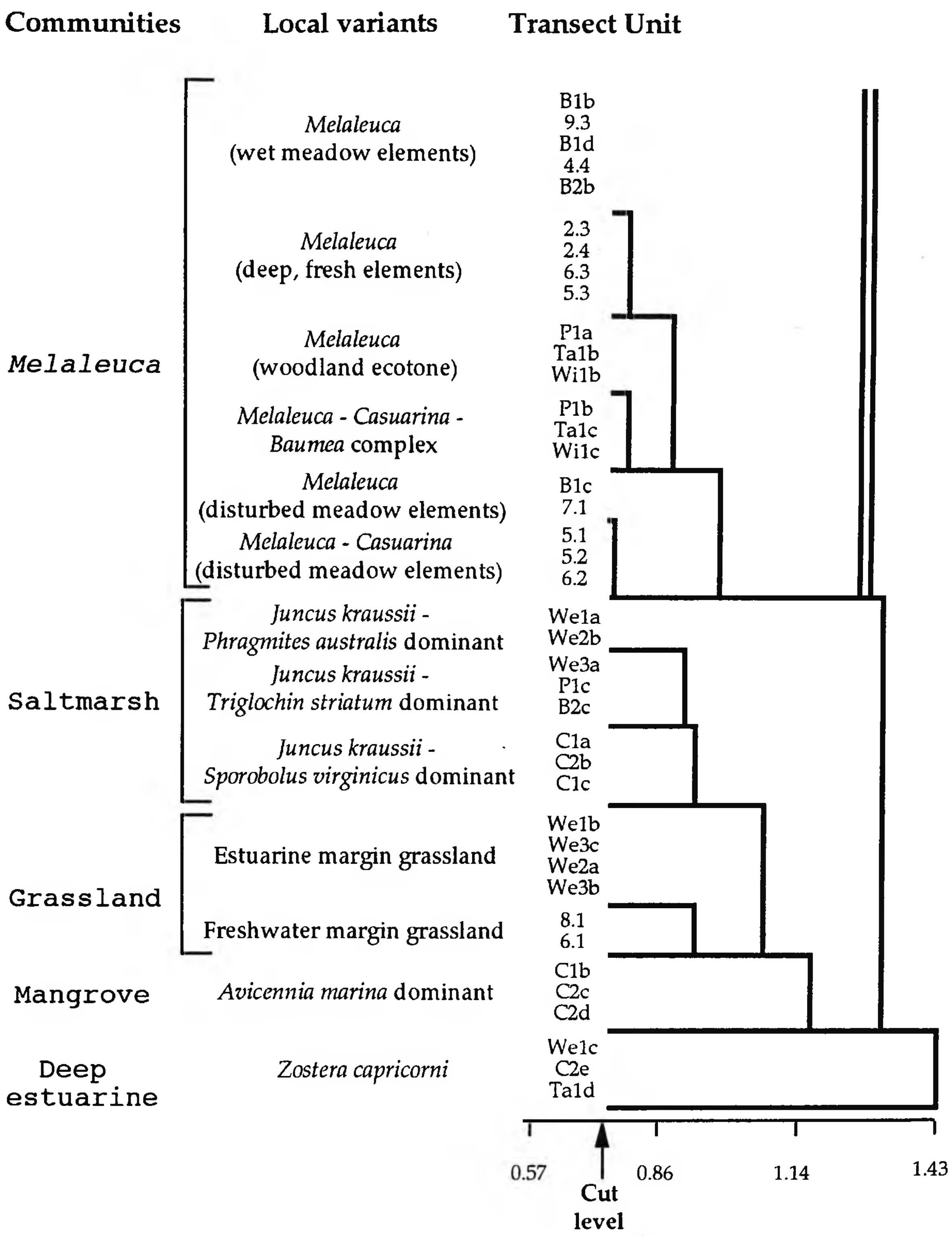


Figure 2.14 (cont'd) Dendrogram derived from cluster analysis of all community transect units encountered at nine South Coast wetlands. Abbreviations for other wetlands are initials: **K**illalea, **T**errara, **B**rundee, **C**rooked, **T**abourie, **W**illinga, **P**attimores and **W**erri; followed by transect number and section of transect ('a' uppermost) i.e. We3c is the 3rd community down the elevation gradient along Transect 3 at Werri Lagoon.

Table 2.3 Pearson correlation coefficients for four vector ordination of community floristics at nine South Coast wetlands with variables indicative of vegetation structure, disturbance and soil-water characteristics.

	Vector 1	Vector 2	Vector 3	Vector 4	Vegetation height	Elevation	Introduced species	Perennial species	Species richness	Soil index	pH
Veg. height	0.006	**-0.494***	-0.348	**-0.494***							
Elevation	0.130	-0.109	-0.089	**-0.391***	0.276						
Introd. sp.	**0.363***	0.203	**0.701***	0.218	**-0.401***	0.115					
Perenn. sp.	-0.015	-0.236	**-0.545***	-0.249	**0.530***	-0.049	**-0.601***				
Sp. richness	0.163	**-0.367***	-0.006	-0.142	0.156	**0.494***	0.103	-0.168			
Soil index	-0.087	-0.109	-0.125	**-0.441***	0.306	**0.638***	0.038	0.126	**0.415***		
pH	-0.366	**0.529***	0.169	**-0.430***	-0.246	-0.260	-0.136	-0.196	-0.273	-0.065	
Salinity	**-0.513***	**0.453***	0.216	**-0.569***	-0.128	-0.168	-0.248	-0.160	-0.336	-0.125	**0.828***

Critical value: $P = 0.001$. $^*P < 0.001$. See text for description of variables. 'n' = 82 community transect units except for salinity and ph where 'n' = 53. Note that stress in the four vector ordination was high (see Section 2.3.3.1).

2.3.3.2 *Characteristics of communities at other wetlands*

The floristics and structure of plant community types could be related to the particular sets of conditions operating in each wetland surveyed (Tables 2.4 & 2.5). In the following descriptions relationships between other wetlands surveyed, and communities and key species of Coomonderry Swamp are emphasised (see also Appendices 5,6 & 7).

Wet meadow communities Ephemeral and wet meadow communities at Coomonderry Swamp were clustered with the brackish wet meadow communities of Brundee, Terrara and Killalea swamps. All these communities were similar in structure, disturbance regime and species richness, and shared a large common pool of short-lived, herbaceous species and Cyperaceae. However the abundance of *Bacopa monniera, Aster subulatus, Hydrocotyle bonariensis* and *Crassula peduncularis* at Killalea wetland indicated the distinctive saline and dunal influence at this site, while the importance of *Cotula coronopifolia, Aster subulatus* and *Triglochin striatum* at Brundee and Terrara were indicative of the brackish inundations experienced by these two wetlands.

Deep, freshwater communities Killalea Swamp was the only other freshwater wetland surveyed and many significant components of Coomonderry Swamp were also found to be important here. These included, *Eleocharis sphacelata, Baumea articulata, Schoenoplectus validus, Typha orientalis, Ludwigia peploides, Azolla filiculoides, Spirodela punctata* and *Myriophyllum simulans.* Notable absences were *Marsilea mutica* and *Melaleuca* spp., while *Chara* sp. was the dominant open water plant.

Grassland (Fig. 2.15) Areas of grazed paddock adjoined some parts of Killalea, Crooked, Brundee and Terrara wetlands, but were only included in transect surveys at Werri Lagoon. At this site the dominant grass species was

Table 2.4 Characteristics of plant communities

Community	Soils	Occurrence at sites	Structure	Main species
Dry Meadow	Sand. Organic content increasing at wetland margin.	Degraded sand dunes adjacent to the eastern margin of Killalea Swamp.	Herb-field. Grassland.	*Hydrocotyle bonariensis* *Cynodon dactylon* *Pennisetum clandestinum* *Isolepis nodosa*
Wet meadow	Peat.	Periodically submerged, unwooded margins of Killalea Swamp and Coomonderry Swamp. Terrara Swamp and Brundee Swamp flats.	Herb-field.	*Isolepis prolifera* *Juncus polyanthemus* *Persicaria decipiens* *Juncus prismatocarpus* *Paspalum distichum* *Senecio madagascariensis*
Deep freshwater	Peat.	Killalea Swamp, Coomonderry Swamp.	Submerged, floating and emergent species of open water in sedgeland, rushland and reedland.	*Eleocharis sphacelata* *Azolla filiculoides* *Marsilea mutica* *Typha orientalis* *Utricularia australis* *Baumea articulata* *Ludwigia peploides* *Chara* sp.
Open-forest	Sandy soils with increasing humic content approaching wetland margin. Lateritic at Killalea.	Higher, dry ground above Crooked, Coomonderry, Brundee, Pattimores, Tabourie and Willinga wetlands.	Open-forest with upper, mid (shrub) and low (herb) layers. Closed-forest (rainforest) in patches at Coomonderry Swamp.	*Eucalyptus botryoides* *Eucalyptus pilularis* *Acacia longifolia* *Breynia oblongifolia* *Pterideum esculentum* *Entolasia* spp. *Lomandra longifolia* *Hibbertia scandens* *Kennedia rubicunda* *Imperata cylindrica*
Swamp mahogany - saw-sedge	Humic to peaty soils.	Eastern margin of Coomonderry Swamp - rarely inundated.	Open-woodland.	*Eucalyptus robusta* *Casuarina glauca* *Gahnia sieberiana* *Hemarthria uncinata* *Villarsia exaltata* *Leptospermum juniperinum*
Sedgeland	Peat.	Central body of Coomonderry Swamp.	Open sedgeland, sedgeland and reedland.	*Baumea articulata* *Baumea arthrophylla* *Villarsia reniformis* *Villarsia exaltata*
Melaleuca	Humic to peaty soils.	Coomonderry and Brundee Swamps. Upper tidal to dry margins of Pattimores, Tabourie and Willinga wetlands.	Scrub and woodland with herb understory.	*Melaleuca ericifolia* *Casuarina glauca* *Baumea juncea* *Persicaria praetermissa* *Viola hederacea* *Entolasia stricta*
Saltmarsh	Saline, organic, sandy or silty loams.	Tidal margins of Werri Lagoon, Crooked River and Pattimores Lagoon. Brundee Swamp flats.	Reedland, open-herb-field and open-grassland.	*Juncus kraussii* *Phragmites australis* *Sporobolus virginicus* *Triglochin striatum*
Grassland	Humic, silty or sandy loams.	Grazed margins at Werri Lagoon and Coomonderry Swamp.	Grassland.	*Pennisetum clandestinum* *Stenotaphrum secundatum* *Casuarina glauca*
Mangrove	Saline, organic loams.	Tidal areas of Crooked River.	Low, open scrub, open herb-field.	*Avicennia marina* *Sarcocornia quinqueflora*
Deep estuarine	Saline, organic loams.	Werri, Crooked and Tabourie estuaries.	Attached, floating species.	*Zostera capricorni*

The various attributes distinguishing communities are shown in Table 2.5. Main species are ranked in general order of importance in terms of distribution and abundance on transects within communities.

Table 2.5 Attributes of communities encountered at nine coastal wetlands in southern NSW.

	Dry meadow	Wet meadow	Deep fresh	Open-forest	Swamp mahogany	Sedge	Melaleuca	Salt-marsh	Grassland	Mangrove	Deep estuary	*P.*
Veg. height	1.18 (0.18) a	1.21 (0.11) a	1.48 (0.10) a	2.44 (0.21) c	2.28 (0.14) bc	1.57 (0.11) ab	2.32 (0.10) c	1.49 (0.13) a	1.61 (0.32) a	1.36 (0.28) a	1.00 (0.00) a	*
Elevation	126 (73) d	7 (4) bc	-47 (11) a	195 (60) d	31 (13) bc	-6 (6) abc	2 (7) bc	-11 (7) abc	41 (16) c	-47 (2) ab	-76 (30) a	*
Proportion introd. taxa	0.40 (0.03) c	0.37 (0.04) c	0.11 (0.04) ab	0.02 (0.02) a	0.01 (0.01) a	0.00 (0.00) ab	0.09 (0.02) ab	0.16 (0.06) b	0.65 (0.10) d	0.00 (0.00) ab	0.00 (0.00) ab	*
Proportion perenn. taxa	0.12 (0.03) ab	0.14 (0.03) ab	0.39 (0.08) c	0.43 (0.02) c	0.48 (0.04) c	0.54 (0.04) c	0.41 (0.05) c	0.28 (0.04) bc	0.12 (0.04) ab	0.31 (0.03) ac	0.00 (0.00) a	*
Species richness	9.5 (1.0) bcd	13.6 (1.6) ab	5.1 (0.8) cf	15.1 (1.4) a	9.2 (1.2) d	5.3 (0.7) cdf	8.3 (1.0) d	5.6 (0.8) cdf	6.8 (1.5) cde	2.6 (0.1) ef	1.0 (0.0) f	*
Soil index	3.0 (0.6) a	1.3 (0.2) cd	1.0 (0.0) d	3.3 (0.3) a	2.0 (0.0) b	1.0 (0.0) d	1.7 (0.1) bc	1.4 (0.2) cd	2.0 (0.0) b	1.0 (0.0) d	1.0 (0.0) d	*
pH	-	5.9 (0.1) a	6.0 (0.1) a	-	-	5.9 (0.1) a	5.9 (0.2) a	6.6 (0.2) b	-	7.0 (0.0) b	7.0 (0.0) b	*
Salinity	-	0.7 (0.6) ab	0.1 (0.0) a	-	-	0.0 (0.0) ab	7.6 (4.0) b	19.2 (4.1) c	-	31.2 (0.8) c	28.3 (8.0) c	*
n	3	9 (5)	15	7	6 (3)	2	20 (13)	8	6	3	3	

Data are means, with standard errors in parentheses, for 'n' replicates of community transect units clustered together within each community (Fig. 2.14). Salinity and pH calculated for inundated community transect units only ('n' in parentheses). Means in each row designated 'a - f' (Fisher PLSD - ANOVA) are not significantly different at $P = 0.05$. Level of significance is * $P \leq 0.0001$. Elevations are in centimetres and salinities are in ppt. Other variables are described in the text.

Figure 2.15 Grassland on the margin of Brundee Swamp.

Kikuyu (*Pennisetum clandestinum)* although *Stenotaphrum secundatum* was also prevalent. Saline elements were interspersed throughout the grassland, particularly in the wettest areas. These included *Juncus kraussii, Leptinella longipes, Tetragonia tetragonoides* and remnant *Casuarina glauca.*

***Melaleuca* communities** (Figs. 2.16 & 2.17) *Melaleuca* scrub at the brackish wetland, Brundee, was similar to that described at Coomonderry Swamp. At both sites, this species continued into standing water forming a dense stratum often taller than 3 m. At Brundee *Melaleuca styphelioides* is a co-dominant woody species in addition to *Casuarina glauca.* Only a few *Melaleuca styphelioides* trees occur at Coomonderry Swamp. Understory species in wetter stands at Brundee were also similar to those found at Coomonderry Swamp despite salinities ranging up to 6 ppt. On drier margins there were numerous affinities with the open-forest vegetation of Coomonderry Swamp, even though parent soils here are lateritic.

Melaleuca ericifolia was the dominant transition species of all relatively undisturbed estuarine wetlands surveyed. As at Brundee, this species remained a significant component on humic soils, perhaps further into woodland than encountered at Coomonderry Swamp. *Melaleuca ericifolia* communities adjoining estuaries did not progress beyond the deeper water margins suggesting an intolerance to continuous saline inundation. The estuarine *Melaleuca ericifolia* communities surveyed, formed a dense 2 m high closed canopy. On drier, sandier soils *Melaleuca ericifolia* commonly occurred with *Eucalyptus botryoides, Acacia longifolia* and *Entolasia stricta.* On wetter, more humic soils *Leptospermum juniperinum, Leptospermum polygalifolium, Centella asiatica, Casuarina glauca, Baumea juncea, Cassytha pubescens, Selaginella uliginosa* and *Hemarthria uncinata* were important

Figure 2.16 *Melaleuca* scrub at Willinga Lake.

Figure 2.17 Saltmarsh, *Melaleuca* scrub and open-forest at Brundee Swamp.

components. On peaty, wet soils *Baumea juncea, Phragmites australis, Juncus kraussii* and *Samolus repens* became increasingly more prevalent. Species richness decreased down the elevation gradient within these communities.

Open-forest communities (Figs. 2.17 & 2.18) *Eucalyptus botryoides* was the dominant canopy species on sandy soils at Lake Tabourie, Lake Willinga, Pattimores Lagoon and Crooked River. On lateritic soils at Brundee Swamp, *Eucalyptus pilularis* was the dominant tall woody species. Mid-story and under-story strata were very similar in all these communities, although a number of species at Brundee - *Acacia falcata, Daviesia ulicifolia, Hibbertia diffusa* and *Eucalyptus ?imitans* - were not found elsewhere.

Dunal, dry meadow communities Disturbed, dryer communities adjacent to the eastern margins of Killalea wetland, supported a number of taxa commonly found on sand dunes. The dominant species found were *Hydrocotyle bonariensis, Cynodon dactylon, Pennisetum clandestinum, Isolepis nodosa, Zoysia macrantha* and *Spinifex sericeus.* Some typical wet meadow species from quadrats on the waterline were also clustered in these communities.

Saltmarsh communities (Figs. 2.17 & 2.19) There was considerable heterogeneity in saltmarsh within and between sites surveyed. *Juncus kraussii, Triglochin striatum* and *Phragmites australis,* were characteristic of grazed saltmarsh at Werri Lagoon and Brundee. *Sporobolus virginicus, Juncus kraussii* and *Phragmites australis* were important components of less disturbed margins. Quadrats containing saltmarsh species were classified with *Melaleuca ericifolia* where the latter made a sharp boundary with open water, while at other sites, saltmarsh formed an understory component of mangrove communities. Open saltmarsh flats at Crooked River were

Figure 2.18 Open-forest at Lake Tabourie.

Figure 2.19 Saltmarsh margin at Pattimores Lagoon.

variously dominated by *Suaeda australis, Juncus kraussii* and *Sporobolus virginicus,* usually in shallower water, and *Sarcocornia quinqueflora* with *Avicennia marina* in deeper water.

Mangrove - saltmarsh communities *Avicennia marina* was only encountered at Crooked River where it occurred with *Sarcocornia quinqueflora, Suaeda australis* and *Sporobolus virginicus.*

Deep estuarine communities Transects at lagoonal sites were terminated in deep water where *Zostera capricorni* predominated.

2.3.4 Discussion

Ordination of transect data from a diverse range of other south coast region wetlands produced only one further variable correlated strongly with changes in floristic composition, this being salinity. It is thus not surprising that both fresh wetland communities and estuarine communities (particularly *Melaleuca* and *Melaleuca/Casuarina* communities), above the influence of continuous inundation, are often similar.

Wet meadow, estuarine pastures and salt marsh Minor differences in wet meadow related to brackish incursions at Brundee Swamp and Terrara Swamp, and to disturbed dunal influences at Killalea. Adam *et al.* (1988) have attributed a decline in *Selliera radicans,* particularly in the Sydney region, to invasion by *Hydrocotyle bonariensis. Hydrocotyle bonariensis* is a dominant component in dry dunal and wet meadow communities at Killalea wetland where *Selliera radicans* is absent. The latter species is found at many nearby wetlands e.g. Lake Illawarra (Yassini & Clarke 1985) and Werri Lagoon, and was plentiful in brackish meadow and saltmarsh at Brundee Swamp and in saltmarsh margins of estuaries surveyed further south where *Hydrocotyle bonariensis* was not encountered (Appendix 5).

Triglochin striatum and *Cotula coronopifolia* occurred only sporadically in fresh, wet meadow at Coomonderry Swamp, but were prevalent in saline and brackish environments surveyed. These observations support the argument of Adam *et al.* (1985) that limiting effects in wetlands more often relate to competition among species rather than an inability to tolerate particular conditions of inundation or salinity. Zedler *et al.* (1995) have suggested that *Triglochin striatum* may have a competitive advantage in areas of saltmarsh where trampling by cattle provides waterlogged recesses. Numbers of this species observed in areas at Brundee Swamp (brackish) and Werri Lagoon (saline) subject to trampling by cattle support this contention.

Both *Triglochin striatum* and *Cotula coronopifolia* are facultative halophytes while other species (e.g. *Lilaeopsis polyantha* and *Villarsia reniformis*) might be considered to be facultative glycophytes (in the sense that they tolerate salinity, but appear to be more competitively limited at saline sites than at freshwater sites). A robust form (phyllodes > 30 cm) of *Lilaeopsis polyantha* was intermittently prevalent in wet meadow at Coomonderry Swamp and this uncommon species has also been recorded at Wingecarribee Swamp in the adjacent highlands (Kodela & Hope 1992) but also, in contrast, at the tidal margins of Werri Lagoon. Coomonderry Swamp supports perhaps the largest population of the uncommon running marsh flower, *Villarsia reniformis,* yet this species was also recorded in smaller numbers at some estuarine and brackish sites (Appendix 5).

Intensive sampling in a one hectare area at the southern edge of Coomonderry swamp detected examples of complex hybridization in taller Juncaceae. Both *Juncus polyanthemus* and *Juncus procerus* (as well as the introduced *Juncus cognatus*) were found at this site beyond their previous known ranges. Hybrids between these two species, between *Juncus* *polyanthemus* and *Juncus usitatus*, and between *Juncus continuus* and *Juncus usitatus* were recorded (L. Johnson Nat. Herb. pers. comm.). Several *Juncus* spp. co-occurred at other sites, and more intensive sampling should elicit further examples of hybridization. For example at Brundee Swamp, *Juncus kraussii, Juncus continuus, Juncus polyanthemus* and *Juncus mollis* co-occurred and Johnson (1993) has previously found hybridization in the latter two species.

Several *Persicaria* spp. are co-dominants in wet meadow at Coomonderry, Brundee and Killalea swamps and an undescribed form of *Persicaria lapathifolia* was recorded for Coomonderry Swamp (P. Kodela Nat. Herb. pers. comm.). Co-occurrence, new forms and the potential for hybridization in this genus have also been noted for wetlands of the Nepean-Hawkesberry system (J. Howell & D. Benson Nat. Herb. pers. comm.) Interactions among co-occurring members of this genus require further examination.

Just as the dynamics of wet meadow precluded finer community divisions, transect analysis at saline sites also supported fewer rather than more divisions within saltmarsh. Cluster analysis of saltmarsh transects produced an erratic grouping of quadrats in response to the mosaic of dominant species encountered. Carne (1989) recorded similar patterns in estuarine vegetation at Minnumurra River (Fig. 1.2). He related these to "geomorphology through the landform attributes of microtopography and substrate composition" which had consequential effects on salinity and waterlogging. Carne (1989) did not differentiate between saltmarsh communities in his work. Zedler *et al.* (1995) also proposed a single saltmarsh community which might be variously dominated by *Sporobolus, Sarcocornia* or *Triglochin.* Clarke (1993) preferred recognition of only five truly saltmarsh complexes (in addition to Mangrove, *Juncus* and associated complexes) even though his study at Jervis Bay (Fig. 1.2) found 16 'communities' analogous to the 25 'communities' described by Adam *et al.* (1988). Clarke *et al.* (1995) later commented on the patchiness of the saltmarsh environment at Jervis Bay. The prevalence of *Juncus kraussii* in assemblages classified as saltmarsh in this report (Fig. 2.14) suggests that *Juncus kraussii* is often an integral member of saltmarsh communities rather than a dominant member of dryer, peripheral communities.

A relatively species-rich assemblage of estuarine pasture species (community transect unit We3a - Fig. 2.14), clustered as saltmarsh, has developed under a regime of continuous grazing and an inundation regime manipulated to mitigate local flooding. It supports an interesting mix of species (Appendix 6), including *Bacopa monniera* and *Isolepis platycarpa,* two species well beyond their previous known southern limits.

Undisturbed freshwater margin Woody species associated with the undisturbed eastern margin of Coomonderry Swamp - *Eucalyptus robusta, Melaleuca* spp., *Leptospermum juniperinum,* and *Casuarina glauca* were also encountered in varying combinations at a number of other wetlands (Appendix 6). However the *Eucalyptus robusta* stand at Coomonderry Swamp was by far the largest and least degraded of any site surveyed. Nor were other sites characterised by a meadow-like understory of *Hemarthria uncinata* and *Villarsia exaltata.*

Open-forest *Eucalyptus* open-forest was the predominant vegetation type on sandier soils above most wetlands surveyed. However the development of littoral rainforest within open-forest seen at Coomonderry Swamp is a rare occurrence (Mills & Jakeman 1995). The only similar stands adjacent to wetland can be found on Comerong Island at the mouth of the Shoalhaven River (Fig. 1.2), and at Jervis Bay on sand dunes where the water table is high (Mills 1995).

2.4 Comparison of Coomonderry Swamp with wetlands of the Jervis Bay Region

Wetlands associated with Jervis Bay were purposely omitted from the present study because of time constraints and because they had received more attention than other South Coast wetlands (Adam & Hutchings 1987; Clarke 1993; Clarke *et al.* 1995; Mills 1995). Mills (1995) provided a comprehensive overview of the natural vegetation of the Jervis Bay area in which he described a number of communities closely affiliated with those found at Coomonderry Swamp. Floristically and structurally, both *Eucalyptus botryoides* and *Eucalyptus pilularis* open-forest communities at Jervis Bay are similar to those found at Coomonderry Swamp. Mills (1995) commented on the usually distinct boundary between the two, and this is also a feature of their occurrence on sand above Coomonderry Swamp. At Jervis Bay littoral rainforest sometimes forms part of this coastal lowland complex (Section 2.3.4). Equivalents of several other coastal communities described by Mills (1995) are found within Seven Mile Beach National Park, immediately east of Coomonderry Swamp, but were not described in the present study.

Casuarina glauca and *Melaleuca ericifolia* communities at Jervis Bay are most often associated with estuarine margins (Mills 1995). Many components of the *Melaleuca ericifolia* substrata are similar to those found at Coomonderry Swamp e.g. *Hemarthria uncinata* and *Entolasia stricta*. However *Casuarina glauca* communities at Jervis Bay indicate the saline influence, with species such as *Samolus repens, Juncus krausii* and *Apium prostratum* (Mills 1995). Sedgelands at Jervis Bay occur in depressions on sandstone soils (Mills 1995). These communities are floristically different to sedgeland at Coomonderry Swamp and are considered by Mills (1995) to resemble those described for upland swamps (Section 2.5). *Eucalyptus robusta* forest - woodland is associated with floodplains and fresh swamps at Jervis Bay (Mills 1995) and is similar to the freshwater - open-forest transition at Coomonderry Swamp, though much less extensive (Braithwaite *et al.* 1995).

2.5 Comparison of Coomonderry Swamp with tableland and upland swamps

The toposequence described for the undisturbed margin of Coomonderry Swamp structurally equates, to some degree, with the *Eucalyptus* woodland - *Banksia* thicket - Restioid/Cyperoid heath - tea-tree toposequences described by Keith and Myerscough (1993) and noted by Stricker and Wall (1995) for upland swamps on tablelands south of Sydney, NSW. This is particularly so where *Melaleuca ericifolia* thickets are found interspersed in deeper areas of sedgeland at Coomonderry Swamp analogous to tea-tree thickets occupying the most waterlogged parts of upland swamps. Keith and Myerscough (1993) in their report also recognized general structural similarities with a related toposequence described by Myerscough and Carolin (1986) for coastal dune fields 200 km north of Sydney. Keith and Myerscough (1993) noted other floristic analogs, all related to a gradient in soil moisture, organic matter and nutrients, for a diversity of temperate heathlands along the eastern coast of Australia.

Despite these structural similarities, floristic composition and species richness at Coomonderry Swamp contrasted greatly with upland swamps. All communities surveyed for this report were much less species rich, and the only affinities in floristics occurred where undisturbed *Melaleuca* communities at Coomonderry Swamp shared some dominants (e.g. *Leptospermum juniperinum* and *Gahnia sieberiana*) with *Melaleuca* thickets of upland swamps. Upland swamps of the Boyd Plateau, Central Tablelands (Kodela *et al.* 1996) are even more floristically distinct.

Greater similarities in species composition were found between Coomonderry Swamp and some freshwater lagoons and reed swamps of 'the coastal division' described by Stricker and Wall (1995) and Ryan *et al.* (1996) although wetlands described by these workers are located further from the coast (>50 km), at intermediate elevations (100-500 m above sea level), and at least 100 km north of Coomonderry Swamp.

2.6 Comparison of Coomonderry Swamp with coastal wetlands of the Sydney region and central coast of NSW

As previously indicated, freshwater dunal wetlands such as Coomonderry Swamp are more commonly found north of Sydney. Structural and floral characteristics of the dune - woodland - fringe forest - swamp transition at Coomonderry Swamp and of the Eurunderee system (Myerscough & Carolin 1986) are very similar. Dry sclerophyll forest communities described by Myerscough and Carolin (1986) have most dominant components in common with the *Eucalyptus pilularis* open-forest of drier, sandy ground above Coomonderry Swamp (Table 2.4), although species associated with heath ecotones at Eurunderee are not found at Coomonderry Swamp. Many dry sclerophyll members described by Myerscough and Carolin (1986) were also noted in the substrata of *Eucalyptus botryoides* open-forest at Coomonderry Swamp. Here also, a number of species listed by Myerscough and Carolin (1986) for vine thicket, headland thicket and rainforest occurred, particularly on more humic soils, and where littoral rainforest is developed within the woodland (see Mills & Jakeman 1995). Although not surveyed for this report, foredune and hinddune communities from both localities had much in common (de Jong pers. obs.)

More significant differences were apparent when communities of the swamp and immediate margins were compared. *Lepironia articulata* and *Melaleuca quinquenervia,* two species not naturally occurring on the south coast of NSW, dictate much of the structure of freshwater wetlands further north. *Melaleuca quinquenervia* within swamp forest of the Eurunderee sand mass appeared to provide a more dense tree stratum than was found in equivalent communities at Coomonderry Swamp. Myerscough and Carolin (1986) did not observe any differentiation of *Eucalyptus robusta* and *Melaleuca quinquenervia* on the basis of water depth. At Coomonderry Swamp *Melaleuca ericifolia* (and *Melaleuca linariifolia* where it occurs) often formed dense thickets in standing water while *Eucalyptus robusta* was generally restricted to the (fluctuating) water margin where fewer *Melaleuca* plants were located. Species common to Swamp Mahogany woodland at both sites included: *Leptospermum juniperinum, Baumea arthrophylla, Baumea articulata, Baumea juncea, Baumea rubiginosa, Gahnia sieberiana, Schoenus brevifolius, Villarsia exaltata* and *Callistemon citrinus.* Formation of hummocks by organic accumulation, with consequent ecotonal development to *Gahnia sieberiana,* was noted by Myerscough and Carolin (1986) and was also typical of undisturbed margins at Coomonderry Swamp (Fig. 2.4).

'Fringe forest' of the lake margins of the Eurunderee sand mass equated to some degree with *Casuarina - Melaleuca* woodland both at Coomonderry Swamp and at other south coast sites surveyed. Understory species in both regions were related to water depth, substrate and salinity. In this case also the dominant, *Melaleuca quinquenervia,* is replaced by *Melaleuca ericifolia* on the south coast of NSW.

The community termed 'swamp' by Myerscough and Carolin (1986) is structurally equivalent to sedgeland and open water communities at Coomonderry Swamp, but species composition differed substantially between the two locations. Only scattered *Melaleuca quinquenervia* and *Banksia robur* trees occurred in swamp at Eurunderree, whereas at Coomonderry, *Melaleuca ericifolia* formed large thickets within the sedgeland. However *Eucalyptus robusta* did not occur within the swamp proper at either location.

Dry sclerophyll communities often associated with coastal freshwater wetlands, such as *Eucalyptus botryoides* and *Eucalyptus pilularis* open-forest, are reasonably well represented in the Sydney region (defined by the Sydney 1:100 000 map sheet - see Benson & Howell 1994). However, in the Sydney area, sedgelands (*Eleocharis* - *Typha* dominated) and wet meadow communities are poorly represented, while only remants of undisturbed freshwater wetlands (*Baumea* dominated) and swamp forest remain (Benson & Howell 1994). Where they are found, these communities closely resemble equivalent communities described in this report, but often contain greater numbers of introduced taxa (Benson & Howell 1994).

2.7 Summary

2.7.1 Regional significance of Coomonderry Swamp This study has confirmed and elaborated on some important vegetation attributes previously indicated for Coomonderry Swamp, as well as identifying some previously not recognized.

Coomonderry Swamp:

(i) **harbours by far the most diverse range of wetland plant communities associated with a single wetland in the region, including:**

(a) the most extensive sedgeland on the south coast of NSW,

(b) the largest stand of *Eucalyptus robusta* (with *Hemarthria uncinata* and *Villarsia exaltata* understory),

(c) probably the largest expanse of the rare *Villarsia reniformis,*

(d) an extensive, species rich freshwater, wet meadow community

(e) floating mat communities

(f) ephemeral communities during draw-down

(g) adjacent littoral rainforest communities

(ii) contains at least 200 plant species some of which:

(a) are rare, regionally rare or poorly conserved including: *Cyperus odoratus, Juncus polyanthemus X procerus, Juncus continuus X usitatus, Juncus subsecundus, Lilaeopsis polyantha, Cardamine paucijuga, Polymeria calycina, Eucalyptus robusta, Melicope micrococca, Cayratia clematidea, Desmodium varians, Goodenia heterophylla* subsp. *eglandulosa, Melaleuca styphelioides* and *Elatine gratioloides.*

(b) are protected: *Blechnum indicum* and *Restio tetraphyllus* subsp. *meiostachyus.*

(c) are at or beyond the limits of their previously recorded ranges, or are a new record for the ecogeographic region e.g. *Cyperus odoratus* and *Juncus polyanthemus* (see Appendix 5 for complete listing).

(xiii) complements the nearby estuarine avian habitats associated with the Shoalhaven River catchment.

2.7.2 Determinants of community distribution Plant community differentiation at Coomonderry Swamp was considered to be related to the structure of vegetation, drainage and nutrient status of soils, and to the influence of anthropogenic disturbance, and disturbance and stress related to inundation change.

Cluster analysis of communities from the eight other local wetlands resulted in the identification of a further four community types with salinity being the major additional environmental component considered to differentiate these groups from those described for Coomonderry Swamp.

2.7.3 Vegetation structure along the elevation gradient The structure of vegetation along the elevation gradient at Coomonderry Swamp was broadly analogous to related toposequences for nearby upland (plateau) wetlands and very similar to variations in structure described for wetland systems of the central coast of NSW. However, floristic composition at Coomonderry Swamp differed markedly from that described for upland swamp communities. There were also substantial floristic differences between plant communities in standing water at Coomonderry Swamp and their equivalents in freshwater swamps of the central NSW coast.

At all the wetland sites there was a decrease in species richness down the elevation gradient.

2.7.4 Regional significance of other wetlands surveyed Important characteristics (over and above intrinsic values recognized for wetlands in general) were noted for some of the other wetlands surveyed. These include:

(i) species-rich estuarine pasture at Werri Lagoon supporting an interesting mix of species including *Bacopa monniera, Isolepis platycarpa, Leptinella longipes* and on the lagoon margin, *Lilaeopsis polyantha.*

(ii) a number of species which are rare, regionally important or well beyond previously recorded limits. These included: *Baumea* *arthrophylla, Restio tetraphyllus* subsp. *meiostachyus, Leptinella longipes* and *Leptospermum juniperinum* at Lake Willinga; *Chamaesyce sparrmanii, Crassula peduncularis, Villarsia reniformis* at Killalea wetland; and large stands of *Juncus polyanthemus* and *Melaleuca styphelioides* at Brundee Swamp.

2.8 Conclusion: Conservation of Coomonderry Swamp

While rigorous faunal assessment is overdue, the present study demonstrates the primary standing of Coomonderry wetland as a reference site for freshwater wetland plant communities in the southern region of NSW. As such, Coomonderry Swamp requires equivalent protection as its counterpart, Jervis Bay, which is now a recognized reference site for marine and estuarine communities (Clarke 1993; Cho *et al.* 1995). Ideally more of the wetland should be included within Seven Mile Beach National Park and it is recommended that procedures be put into place to have Coomonderry Swamp listed under the RAMSAR convention (Section 5.5).

It is most important that the recommendations listed by the consultants, Mitchell McCotter & Associates Pty Ltd (1991 Ch. 6), be adhered to by Shoalhaven City Council as development of the catchment area proceeds. These measures included: (i) the setting aside, fencing and restoration (where needed) of buffer zone; (ii) sewage disposal methods which take account of the limited capacity of soils to purify effluent; (iii) pollution controls being included in subdivision design (iv) enlargement of the area zoned Environmental Protection 7(a) to include any land dedicated to the Council and proper management being implemented to enhance the areas' environmental attributes; (v) adoption of minimum two hectare lots where subdivision is allowed.

Eucalyptus robusta

Chapter 3 Vegetation dynamics at Coomonderry Swamp.

3.1 Introduction

Understanding the causes of vegetation change in wetlands is fundamental to wetland conservation and restoration and has become an important focus of both Australian and overseas research. This chapter explores spatial and temporal vegetation dynamics at Coomonderry Swamp (Fig. 3.1). Change in herbaceous vegetation is examined in more detail and a schematic model is developed which indicates potential cyclic and successional responses.

Spatial variation The first investigation deals with the spatial integrity of zonations. Zones of vegetation (primarily determined by water depth) have been well documented in the wetland literature (e.g. Grace & Wetzel 1981; Spence 1982; Keddy 1983, 1984; Snow & Vince 1984; Wilson & Keddy 1985; Welling *et al.* 1988). However it may be that in some studies the subjective choice of the position of transects, or placement of quadrats, will correspond to where zonations are visually best defined. There is a possibility in these circumstances, and where there has been insufficient spatial replication, that defined boundaries over-emphasise clonal outgrowths (i.e. boundaries result from rapid colonization of certain species after disturbance) at the expense of accurately determining biotic and abiotic factors which are generally limiting distributions of species.

The objective was to examine spatial variation in plant species distributions along both the wet meadow transition and the *Melaleuca* - open-forest transition at Coomonderry Swamp (at Sites 1,2 & 3, Fig. 3.2). The key question was: Is there spatial uniformity in the boundaries defined in Chapter 2 for communities along these transitions (i.e. are boundaries broadly equivalent in species, depth and soil type)?

Vegetation dynamics at Coomonderry Swamp

- **Spatial variation**
  Do plant species changes along the elevation gradient vary spatially within structurally similar units of vegetation?
- **Temporal dynamics**
  - **Long term (50 years)**
    What broad scale changes have resulted from anthropogenic impacts?
  - **Short term (3.5 years)**
    - **Changes along the open-forest - *Melaleuca* transition**
      How substantial are the changes occurring in understory species within open-forest, Swamp mahogany - saw-sedge and *Melaleuca* communities?
    - **Changes along the wet meadow - open water / mud transition**
      - **The dynamics**
        How substantial are temporal variations in community attributes (i.e. plant species abundance and distributions, plant species richness)?
        Do plant communities change through time?
      - **Potential abiotic causes**
        Can edaphic factors determining change in vegetation be identified?
        Can cyclic change in herbaceous vegetation be predicted from the application of a simple qualitative model?
      - **The role of biotic factors**
        Can plant interactions be identified and do they vary through time?
        Do interactions vary in response to the transition along the gradient from mesic to harsh conditions?
      - **Ecological profiles**
        Are there species, or suites of species which can be practically used to define boundaries in a dynamic wet meadow environment dominated by herbaceous plants?

Figure 3.1 Components of research into vegetation dynamics at Coomonderry Swamp.

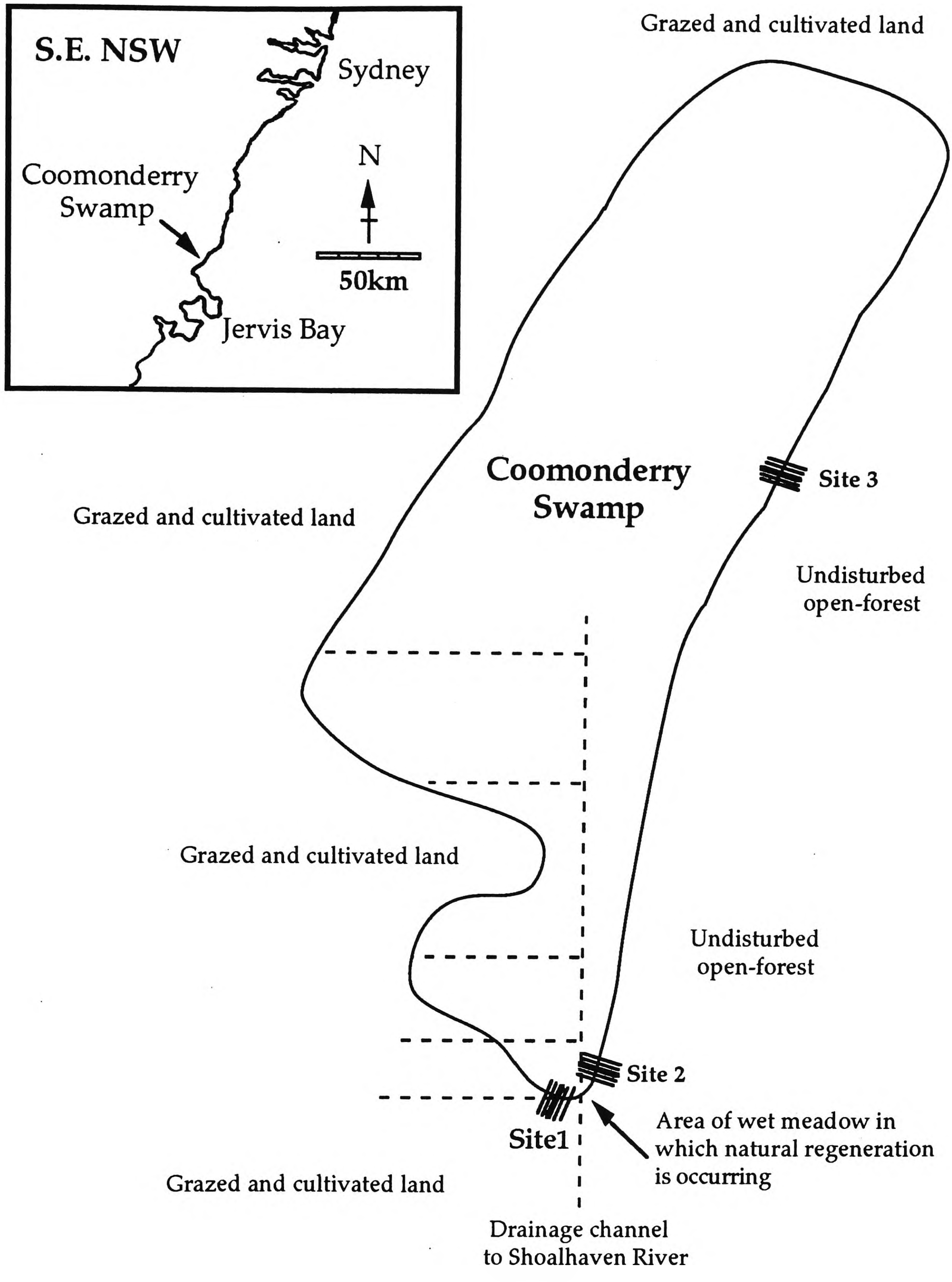


Figure 3.2 Location of sites for investigation of spatial and temporal vegetation dynamics. Site 1: wet meadow - open water/mud transition. Sites 2 & 3: open-forest - *Melaleuca* transition. Main drainage channels shown by dashed lines.

Temporal dynamics Long term changes in vegetation structure, and the boundaries of major vegetation types, were evaluated at Coomonderry Swamp from the aerial photographic record. An investigation of the responses of plant species and communities to seasonal change and variations in inundation over 3.5 years was also carried out. Coomonderry Swamp is a large wetland supporting a broad diversity of communities (Ch. 2) and the logistical constraints of the study did not allow temporal surveys of transects to be conducted in all vegetation types. In fact, wetland models are often based or tested on small wetlands, or riparian systems, with a restricted range of herbaceous life forms (e.g. Poiani & Johnson 1993). Thus detailed examination of temporal dynamics at Coomonderry Swamp was confined to a wet meadow - open water/mud transect at the southern margin (at Site 1, Fig. 3.2) termed 'the wet meadow transition'.

There were other important reasons for understanding the processes at this part of the wetland: (i) this wet meadow area is adjacent to the most intensive land use above the wetland margin i.e. turf cultivation (Figs. 1.3, 3.12), (ii) wet meadows are among the most species rich communities at Coomonderry Swamp and in other wetlands (Ch. 2), and it would be interesting to understand more about species interactions contributing to diversity, (iii) the greatest variation in inundation occurred in this part of the wetland (Fig. 3.3), and yet (iv) the hydrology here may have changed because drainage canals (Fig. 3.2) are no longer maintained, (v) the wet meadow was previously cleared and grazed and thus represents the type of vegetation forming the starting point for further woody plant restoration, here and at other degraded wetlands in the region and (vi) natural woody plant regeneration is occurring in parts of the wet meadow following cessation of grazing (Fig. 3.2).

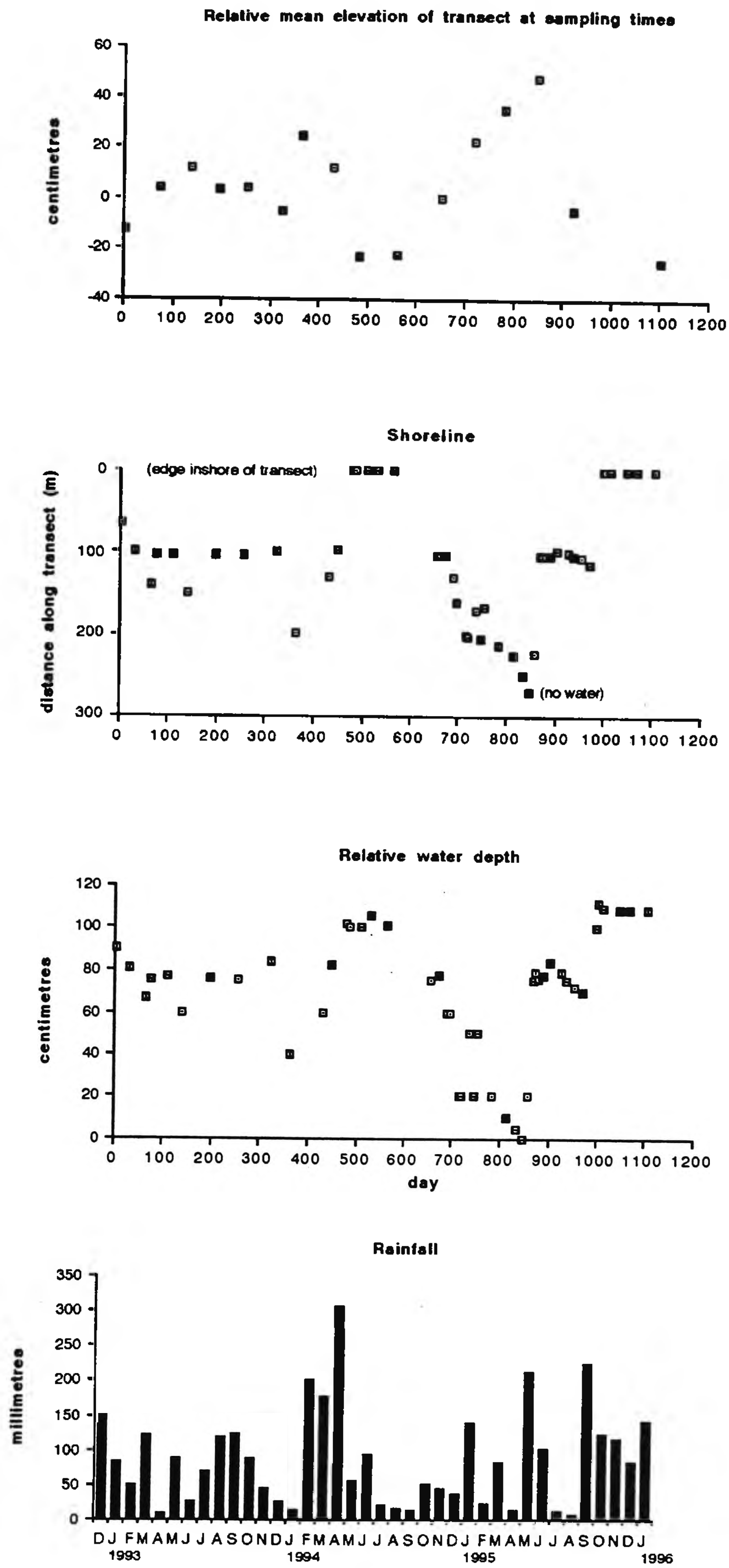


Figure 3.3 The relationship between rainfall and inundation at Site 1 (Transect 1), Coomonderry Swamp. Water depths and elevations are relative to a permanent marker. Mean elevations are for all contiguous quadrats along Transect 1.

A less detailed survey of temporal vegetation change was made along the undisturbed eastern margin of the wetland (at Site 2, Fig. 3.2) to record the degree of change in understory species of the Open-forest and Swamp Mahogany - saw-sedge communities and, in standing water, below the *Mealaleuca* community.

Benefits of a 3.5 year study In terms of conservation, three years of data provide a much broader baseline record than initial description because patterns of cyclic change may be recognized and more complete species lists compiled (Section. 1.6). Of course the data set needs to be of a longer duration to allow identification of directional changes (which might result from anthropogenic disturbance) (e.g. van Groenendahl *et al.* 1996), or to apply quantitative models of directional change (e.g. Poiani & Johnson 1993).

There is a clear link between restoration goals and secondary successional processes i.e. vegetation is established in created and restored wetlands to accelerate or direct succession towards a desired vegetation type (Section 4.2.4). It is necessary to understand prior to planning for restoration the range of vegetation types possible for a system, in response to varying combinations of inundation and season. The 3.5 yr of record achieved in this study allowed a broad range of conditions, with associated species compositional outcomes, to be experienced.

For the purposes of inventory, mapping and identifying directional changes to major vegetation boundaries, aerial photographic techniques (e.g. Blackman & Locke 1985) and remote sensing methods (e.g. Johnston & Barson 1993) have been used. However these methods require careful standardization of images and identify only very broad-scale changes. They do not provide sufficient resolution (cost effectively) to identify dynamics at finer scales of distance and time, which are important, rarely studied and are therefore the primary focus of this work. As indicated, aerial photographic records were available for Coomonderry Swamp over a fifty year period and these were used to evaluate the dynamics of major vegetation boundaries over the longer term.

Appropriate models Day *et al.* (1988) explained that there was a continuum of vegetation models from site specific, multivariate, species-orientated descriptions to models of very general processes (e.g. Grime 1979). Like Day *et al.* (1988), this research also explores varying degrees of generality, beginning with description at a single site, then comparisons with other sites in NSW (Ch. 2), and in this chapter, an examination of processes and of models based on these processes. In particular, the pattern of vegetation change at Coomonderry Swamp will be tested against the qualitative model of allogenic succession developed by van der Valk (1981) (Fig. 3.4). While many models are too specific because they incorporate gradients irrelevant to the present study (e.g. Day *et al.* 1988), some processes incorporated in them (e.g. pre-emptive competition, inertial effects and seasonal senescence) may be identified as components of vegetation change in wet meadow at Coomonderry Swamp. Questions pertaining to this study of vegetation change are: (i) How significant are the temporal variations in community attributes? (ii) Do communities change through time? (iii) Can edaphic factors determining changes in vegetation be identified? (iv) Can cyclic vegetation change be predicted from the application of a simple qualitative model?

The role of biotic factors in determining zonations Van der Valk's (1981) model intentionally does not include species interactions, yet many studies have demonstrated the roles of edaphic and biotic factors in determining zonations and species densities along wetland gradients (e.g. Grace & Wetzel

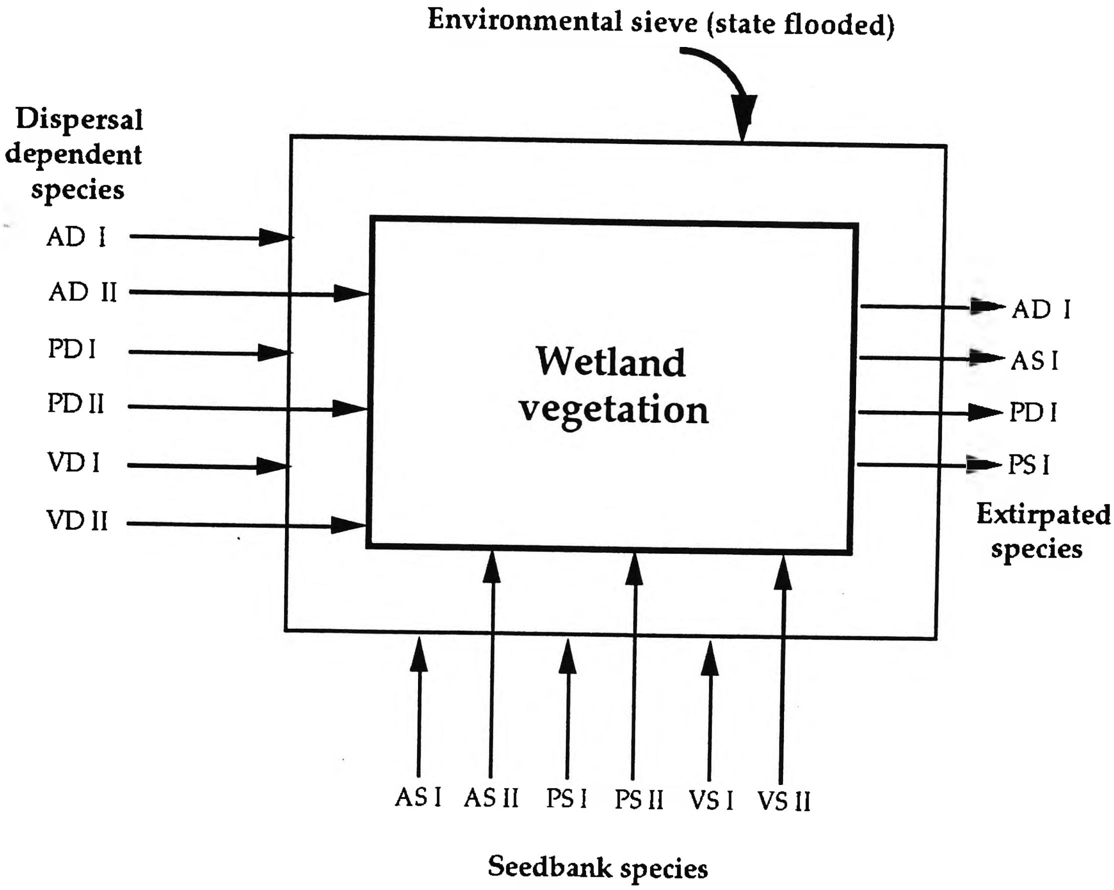


Figure 3.4 A model of allogenic succession in wetlands (van der Valk 1981). According to this model, the physical environment primarily determines which species may become established, and which may not survive. For example, only those species with the appropriate life history features are able to establish during flooding while others may be eliminated. Conditions during drawdown favour the establishment and extirpation of species with different life history features. 'A' - annual species; 'P' - perennial species with a limited life-span; 'V' vegetatively reproducing perennials that do not have a limited life-span; 'S' - seedbank species with long-lived seeds or propagules; 'D' - dispersal dependent species with short-lived seeds and/or propagules. 'Type I' species only establish during drawdown. 'Type II' species only establish during flooding. Refer to van der Valk (1981) for a detailed description of the model and examples of its application to wetland studies.

1981; Keddy 1983; Snow and Vince 1984; Taylor & Dunlop 1985; Wilson & Keddy 1986a). For example, Snow and Vince (1984) showed that edaphic factors played a greater role in harsh saltmarsh environments and that competition was more important in less stressful saltmarsh environments. Variation in competition along gradients has been shown for other systems (e.g. abandoned pastures, Reader & Best 1989), and was generally predicted by Grime's (1973) 'hump-backed' model of species density along gradients. This model suggested: (i) a decrease in species richness along the gradient from a more benign to a harsher (more stressful and/or greater disturbance) environment and (ii) a decrease in species richness where dominance developed. Grime (1985) indicated the close relationship between his 'hump-backed' model and his 'competitor-stress-ruderal' (CSR) model. Grime (1985) argued that plants with particular CSR strategies were more likely to occupy particular regions on gradients indicated by the 'hump-backed' model. For example species-rich vegetation (the 'hump' of the model) would be occupied by the majority of plants which are neither potential dominants nor capable of surviving in extreme habitats. Several workers investigating species coexistence along wetland gradients have subsequently incorporated examination of life strategies and, in doing so, have made use of Grime's (1974, 1979) CSR model (e.g. Wilson & Keddy 1986b; Day *et al.* 1988; Shipley *et al.* 1989; Gaudet & Keddy 1995).

The complexity of plant interactions has become apparent in several recent wetland studies. Various researchers have pointed to fluctuations in competitive success of wetland plant species in response to environmental variation in general (e.g. Keddy *et al.* 1994; Bonis *et al.* 1995; Rejmankova 1996), or with life stage events (e.g. Shipley *et al.* 1989). Others have differentiated between the competitive effect and the competitive response of wetland plants (Keddy *et al.* 1994).

Bertness and Callaway (1994) suggested that there had been a de-emphasis in the recent literature of the role of facilitation and predicted that facilitation should be greater in harsh conditions and competition greater in mesic conditions. Bertness and Shumway (1993) had previously demonstrated the relative influences of these biotic factors in saltmarsh. Parsons (1996) has recently argued that competition, from an evolutionary perspective, should be restricted to benign habitats. His argument was consistent with the earlier suggestion of Parrish and Bazzaz (1982) that selection to reduce competition should be more important for late successional species than for early successional species.

In this chapter consideration of biotic effects is restricted to the following questions: (i) Can significant interspecific interactions be identified?, (ii) Do they vary through time? (iii) Is there support for the model of Bertness and Callaway (1994) which suggested a greater role for facilitation under harsh conditions and for competition under stable conditions?

Ecological profiles Investigating the ecology of plants over a diversity of conditions allows ecological profiles of 'key' species to be compiled, and this is important for restoration and creation purposes (Sections 1.7 & 5.4.2). Henceforth, I will use the terms 'key' or 'dominant' to refer to species which are well distributed, consistently abundant and contribute strongly to the structure of vegetation (see Section 3.4 & Table 3.3). Such species are likely to be chosen for use in wetland restoration and creation projects. The term 'secondary' will be used for more transient species which may have less importance in determining the distribution and abundance of other species (e.g. Table 3.4).

Another potential benefit of compiling ecological profiles might be the identification of herbaceous plant species, or a suite of herbaceous species, which show temporal constancy in a fluctuating environment. In particular, such species at the upper margins, may be useful for delineating boundaries and this is a primary concern of authorities dealing with legislative wetland protection (Adam *et al.* 1985; Barson & Williams 1991; Mitch & Gosselink 1993, Ch. 2).

The final objective of this chapter is to construct ecological profiles for species of the wet meadow transition based on the spatial and temporal data accumulated in this research and that available from other sources. I will then evaluate their value as indicators of the wet meadow - terrestrial boundary.

General aim While several research questions are explored in this chapter (Fig. 3.1), the unifying aim is to understand more of wetland function by investigation of vegetation dynamics at Coomonderry Swamp. Both temporal and spatial analyses allow verification of the community description presented in Chapter 2. The long-term photographic record shows the extent of human induced impacts and may give indications of successional change. The 3.5 year temporal study records changes in herbaceous vegetation and explores the potential causes of observed dynamics. Understanding the processes which determine vegetation change is an important prerequisite to work on wetland restoration, the subject of Chapter 4 of this thesis.

3.2 Spatial variation at Coomonderry Swamp

3.2.1 Aim

To determine if plant species changes along the elevation gradient vary spatially within structurally similar units of degraded and undisturbed vegetation.

3.2.2 Method

Sites for this investigation corresponded to the locations of transects 1,2 and 3 described in Section 2.2.2.2, but were begun 120 m, 70 m and 20 m further down the gradient respectively, since interest here was in zonational change only. At each site, five parallel belt transects (1 m width) separated by 20 m, were situated along the elevation gradient (Fig. 3.2). Transect length was again dependent on the rate of change of vegetation along the gradient (Section 2.2.2.2): Site 1 (Transects 1A-1E) 150 m; Site 2 (Transects 2A-2E) 120 m; and Site 3 (Transects 3A-3E) 100 m. Estimates of percentage cover in six groups (0, 1-20, 21-40, 41-60, 61-80, 81-100) were made for all plant species in contiguous, 2 m x 1 m quadrats along each transect. Elevations along each transect at Site 1 were measured every 2 m as described in Section 2.2.2.2 and could be related. At Sites 2 and 3 the density of vegetation prevented determination of the elevation gradient on all transects. However the elevation gradients for Transects 2C and 3C are the same as those shown in Fig. 3.21 and Fig. 2.4 respectively.

Direct gradient analysis was carried out for five key species along each transect at each site. Four of these species were the same for Sites 2 and 3, to allow examination of spatial patterns over a much larger area (approximately 2 km). However, vegetation differed markedly at the lower end of the transition with Site 2 dominated by *Melaleuca ericifolia* and Site 3 dominated by *Baumea articulata.* Although multivariate data were collected, analysis of the type described in Sections 2.2 & 3.3 was beyond the scope of the present study but will be one of a number of researches continued on completion of the thesis.

3.2.3 <u>Results</u>

Site 1, Wet meadow - open water transition In Section 2.2.3.1 (Appendix 4), two communities were defined along Transect 1C: a wet meadow community and a deep freshwater community termed '*Marsilea* complex'. Inspection of Fig. 3.5 stongly suggests that Transects 1A,B,D and E conformed to the same pattern. In all cases, *Isolepis prolifera, Paspalum distichum* and *Pseudoraphis paradoxa* and *Juncus polyanthemus* (and hybrids - Section 2.3.4) were strong components above the water line while *Marsilea mutica* was confined to very wet or inundated ground.

There were also consistencies in the abundance and distribution of individual species within the wet meadow community. *Isolepis prolifera* was most abundant on all transects at an intermediate elevation. *Juncus polyanthemus* although broadly distributed was most strongly represented at drier elevations. *Pseudoraphis paradoxa* was most dominant at drier elevations, while the realized niche of *Paspalum distichum* incorporated a region of fluctuating inundation (Fig. 3.3).

Most other species also conformed to distinctive bands. Within the wet meadow these included *Ranunculus inundatus, Persicaria decipiens, Hydrocotyle peduncularis* and *Juncus procerus. Marsilea mutica* was the only significant component in deep water at this time, although on other occasions *Azolla filiculoides* and *Spirodela punctata* occurred.

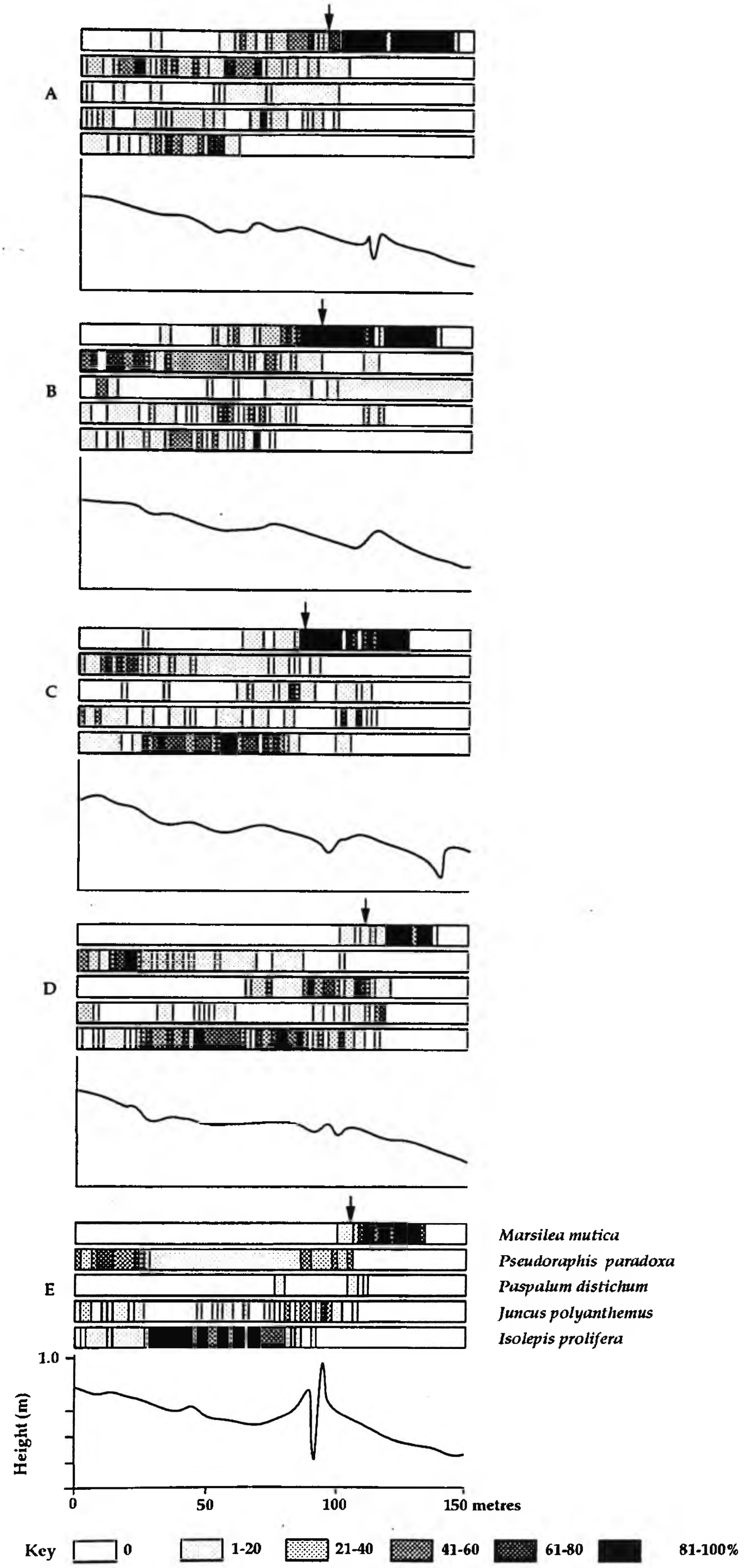


Figure 3.5 Spatial variation in the distribution and abundance of five plant species at Site 1, a wet meadow - open water transition, at Coomonderry Swamp. Percentage cover was estimated along transects A - E spaced at 20 m intervals. Vertical arrows show the water's edge. Heights are above an arbitrary datum.

Site 2, Open-forest - *Melaleuca* scrub transition Zonations are well defined at this site (Fig. 3.6). Communities termed 'Open-forest' (dominant species *Eucalyptus botryoides*) 'Swamp Mahogany - Saw-sedge' (dominant species *Eucalyptus robusta, Gahnia seiberiana* and *Hemarthria uncinata*) and '*Melaleuca* scrub' (dominant species *Melaleuca ericifolia*) (Fig. 2.5, Appendix 4) are clearly recognizable in the field along all five transects.

It was evident that the distributions of some species were pre-emptively determined by the vegetative spread of others. For example, within the Swamp Mahogany - Saw-sedge community *Hemarthri uncinata* occupied open patches around stands of *Gahnia seiberiana.*

Site 3, Open-forest - sedgeland transition Once again the boundary between inundated and 'dry' margin was floristically well defined (Fig. 3.7). Distributions of key species (and secondary species which are not shown) above the wetland margin at Sites 2 and 3 were similar. A further complexity at Site 3 resulted from the presence of littoral rainforest which impinged on the distribution of *Eucalyptus botryoides.* Some *Eucalyptus robusta* trees were found within the shallower margins of the sedgeland, whereas at Site 2 they were displaced almost immediately at the water's edge by *Melaleuca ericifolia.*

3.2.4 Discussion

In the introduction to this chapter I argued that zonations in wetlands could be misinterpreted with insufficient spatial replication, because sharp boundaries between stands of different species are determined by the extent of vegetative spread (which may or may not be pre-emptively limited) as well as by edaphic factors. The problem of defining zonations (and

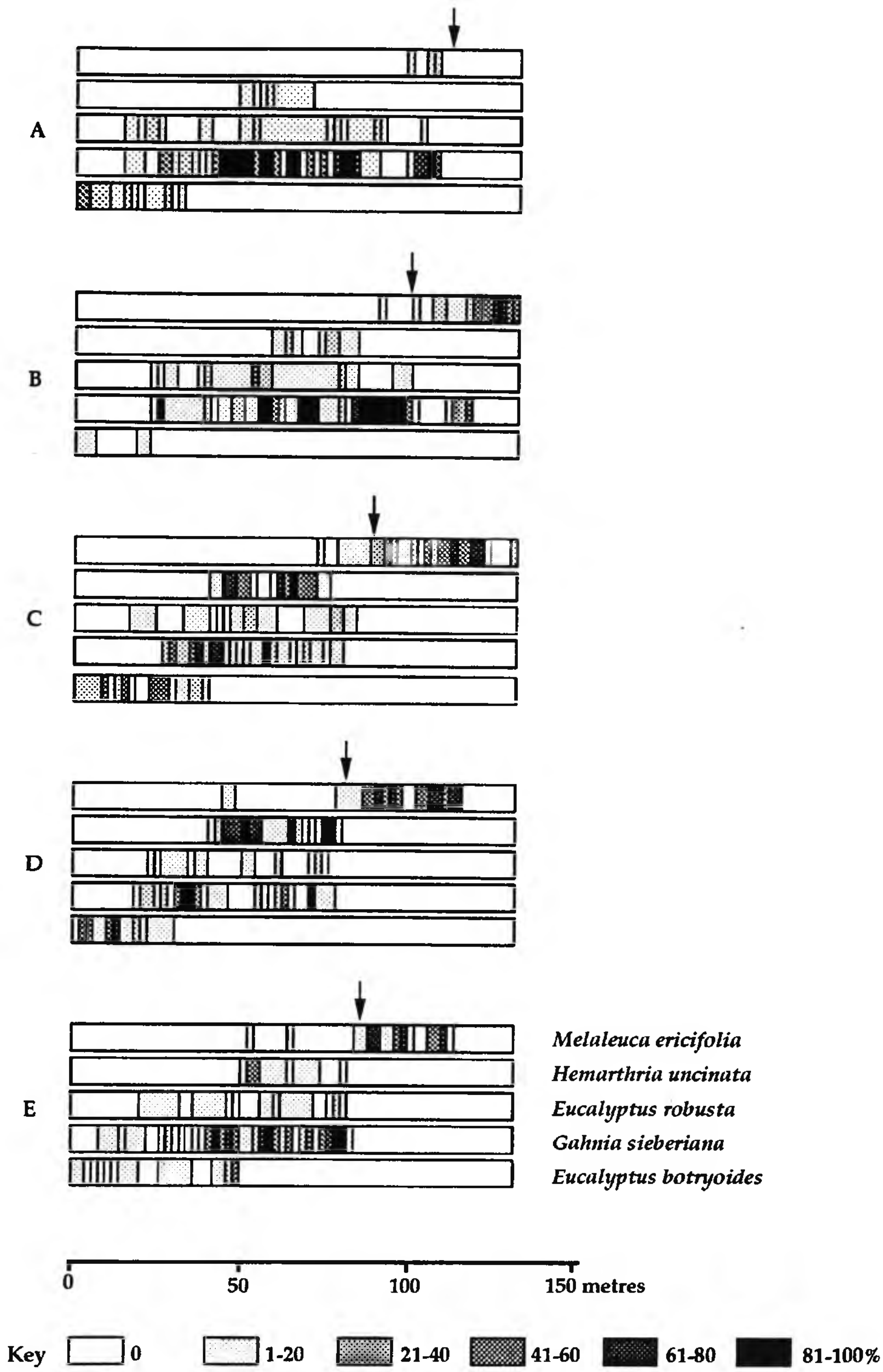


Figure 3.6 Spatial variation in the distribution and abundance of five plant species at Site 2, an open-forest - *Melaleuca* transition, at Coomonderry Swamp. Percentage cover was estimated along transects (A - E) spaced at 20 m intervals. Vertical arrows show the water's edge.

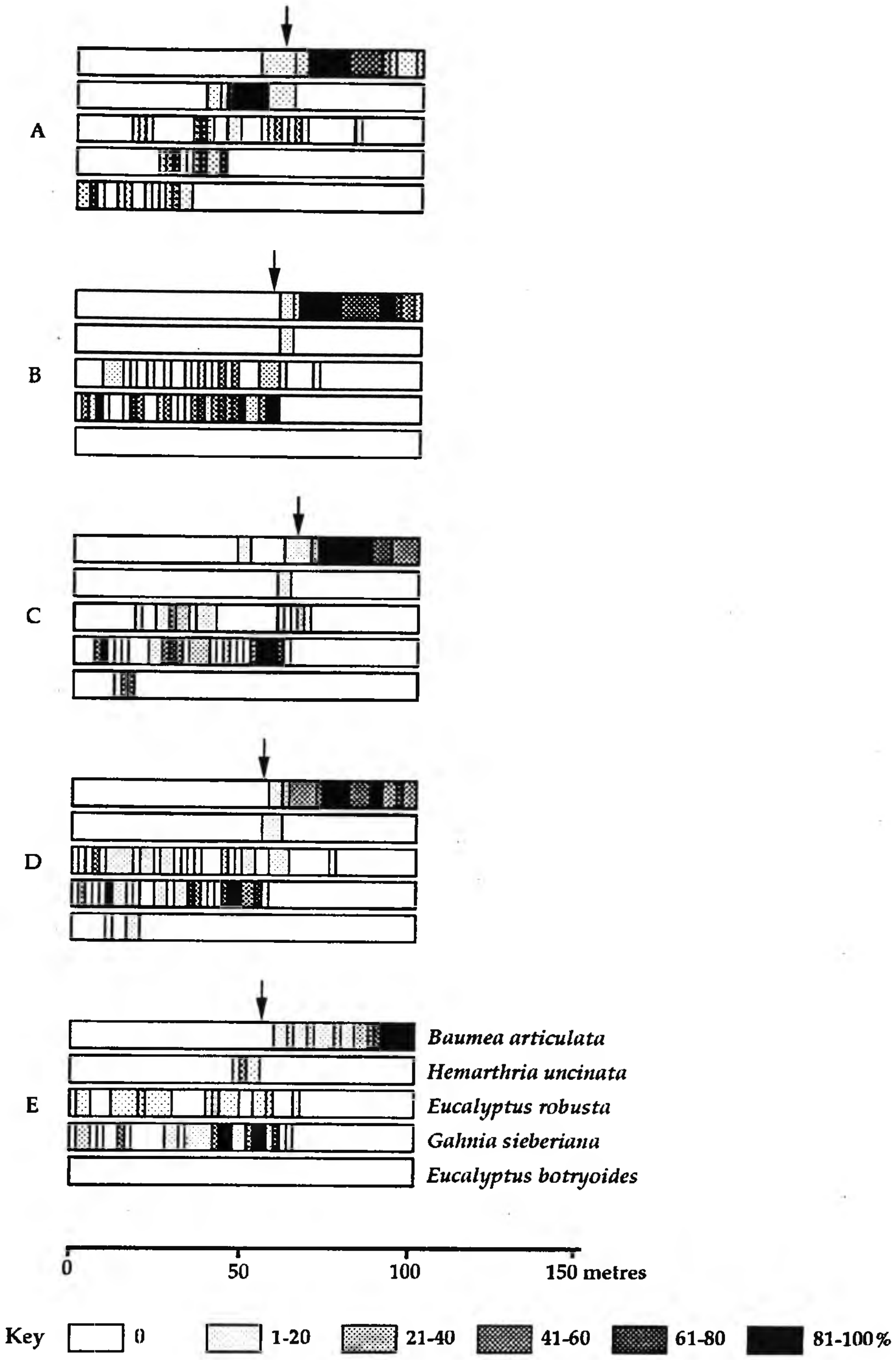


Figure 3.7 Spatial variation in the distribution and abundance of five plant species at Site 3, an open-forest - sedgeland transition, at Coomonderry Swamp. Percentage cover was estimated along transects (A - E) spaced at 20 m intervals. Vertical arrows show the water's edge.

communities) is well illustrated in studies of saltmarsh in NSW (Clarke 1993; Zedler *et al.* 1995). In saltmarsh a mosaic of vegetation, determined by a complexity of factors e.g. microtopographic variation, competition, clonal outgrowth, disturbance patterns (see Section 2.3.4) overlies the zonation, which can only be properly recognized by sufficient spatial sampling.

Similarly, it was not expected that such a degree of uniformity would be found in the spatial distribution of species along the wet meadow - open water transition at Coomonderry Swamp. It was predicted that zonation would be diffused by the variability in the inundation regime and the patchiness of the environment. The ground undulates along the slight gradient (Fig. 3.5) and soils are intrinsically uniform (Fig. 4.4 & Table 4.1) and are thought to differ markedly only when inundated.

It was because wetlands, particularly those dominated by short-lived species are so dynamic that plant communities at Coomonderry Swamp were differentiated at a relatively course level (Section 2.2.4). This survey confirmed that the wet meadow- *Marsilea* boundary was spatially discrete at the time of sampling. Temporal analysis (Section 3.3) will indicate whether (i) this boundary becomes diffused under varying inundation patterns and (ii) whether wet meadow should have been further subdivided in Section 2.2 into a dryer herb - grass association and, at lower elevation, into a Cyperaceae - Juncaceae subgroup.

Along the wooded margin at Sites 2 and 3 the obvious water's edge corresponded to a very discrete floristic boundary. Figure 3.6 (and to a lesser extent Fig. 3.7) confirms the division of vegetation above the undisturbed margin into the two communities, Open-forest and Swamp Mahogany - Saw-sedge (Section 2.2.3). There is spatial uniformity in the distributions of

Gahnia sieberiana, Eucalyptus robusta and *Hemarthria uncinata* within and between the two sites.

Although each of these communities has distinct floristic and structural characteristics related primarily to soil type (Tables 2.4 & 2.5), the species themselves intergrade gradually (Figs. 3.6 & 3.7) along with the gradual change in the soil. It is in these circumstances, where there is a continuum of variation that the precise definition of communitiy boundaries becomes arbitrary and lends itself well to identification by an objective method of pattern analysis (Section 1.5).

Future studies will need to investigate those factors of the environment determining spatial distributions of (i) littoral rainforest within open-forest (but see Mills & Jakeman 1995) (ii) dominants along the undisturbed freshwater margin (listed in Table 2.4) and (iii) *Melaleuca* spp., *Baumea* spp. and, in some areas, *Casuarina glauca* within standing water.

3.3 Temporal vegetation dynamics at Coomonderry Swamp

This section of the thesis deals with both long term changes to the whole wetland and short term changes along two different transitions. A number of approaches were necessary to identify plant species responses to seasonal change and variation in inundation (Fig. 3.1).

3.3.1 <u>Aims</u>

To identify broad scale changes and long term anthropogenic impacts on Coomonderry Swamp and its catchment.

To determine if plant communities change through time. How significant are temporal variations in community attributes i.e. plant species abundance and distributions, plant species richness?

For the wet meadow transition (i.e. Transect 1 wet meadow to open water/dry mud):

To investigate the potential abiotic causes for observed vegetation dynamics at the community level and at the species level.

To apply a model of cyclic vegetation change in wetlands to the data set. Are the dynamics of herbaceous vegetation able to be predicted?

3.3.2 Methods

3.3.2.1 *Long term vegetation dynamics*

Aerial photographic records for Coomonderry Swamp were available for a forty seven year period. Where possible these were examined stereoscopically and at magnification. Descriptions of major vegetation boundaries and land use based on aerial photographs are presented for six dates: 1949 (1:30000 black & white), 1961 (1:40000 black & white), 1972 (1:20710 colour), 1981 (1:25000 colour - NSW coastal wetlands), 1986 (1:25000 colour - NSW coastal wetlands) and 1993 (1:25000 colour - coastal surveillance). The 1981 photo was the most clearly defined (Fig. 3.11) and was used as a reference for identification of vegetation (c.f. Adam *et al.* 1985) along with the 1993 record for which vegetation stands could be confirmed by ground survey and by referral to Figure 1.3.

3.3.2.2 *Short term vegetation dynamics - survey design*

Temporal investigation of vegetation change was carried out over three years, at Transect 1 along the wet meadow transition, and at Transect 2 along the open-forest - *Melaleuca* transition (Fig. 2.1). These locations were equivalent to Sites 1C and 2C of the spatial study described in Section 3.2 (Fig. 3.2). Transect 1 was always started at the same upper point, but varied in length from 200 m to 234 m, depending on the extent of vegetation at the low end of the gradient. Here sampling was curtailed either in open water or within visually homogeneous stands of vegetation on mud or shallow water. Transect 2 was always started at the same point within open-forest and was terminated after 210 m within *Marsilea mutica* or open water. Due to flooding, the last survey (Jan. 1996) was curtailed at 180 m within *Melaleuca ericifolia*.

Estimates of percentage cover (0, < 10%, ≥ 10%) were initially made for all plant species in contiguous, 2 m x 1 m quadrats along each transect. Difficulties were encountered in (i) estimating percentage cover where plants showed winter senescence - only 'green' cover was recorded, and (ii) distinguishing among some species of Poaceae, *Persicaria* and *Juncus*. After 12 months, increased competency enabled percentage cover to be confidently estimated to the nearest 10 %.

Transect 1 was surveyed approximately every two months for 2.5 years beginning in January 1993. The study is continuing with surveys at six monthly intervals, and hence the two final records extend the data set to 3.5 years. Vegetation along the undisturbed margin of Coomonderry Swamp is dominated by woody species. It was expected that temporal variations would be much less dramatic and that this survey would only show changes to understory species. Transect 2 was surveyed every four months for one year (1993), and again after another two years (Jan. 1996).

Water depth and shoreline were recorded at regular intervals for the duration of the project (Fig. 3.3). Rainfall and temperature records were obtained from the Bureau of Meteorology for Station 06080, Greenwell Point (34^o 55'S; 150^o 44'E). Soils characteristics are given in Figs. 2.3 & 4.4 and Table 4.1. Plant species richness was recorded at the 10m^2 scale (five quadrat interval).

3.3.2.3 *Analyses of temporal change along the wet meadow transition*

There are two major difficulties with evaluating vegetation dynamics over time. Firstly, no one method of presentation will adequately summarize the data set. Secondly, the inertia of the system (response lag-time) masks the dynamics. Thus a range of descriptive approaches was used and temporal variation in vegetation was evaluated at three levels: (i) the whole transition, (ii) the community, and (iii) the species level.

(i) **Whole transition dynamics** Comparisons between temporal transect units (termed 'samples') was achieved in four ways. Firstly, direct gradient analysis (DGA) was used to compare sequential samples. Secondly, photographs were taken for some samples at 0, 100, 160 and 180 m along the transect so that visual comparisons could be made between wet and dry summers and winters. Thirdly, a clustering strategy was used to group time units based on species compositional similarity in quadrats along the transect. Lastly, HMDS ordinations in 2, 3, and 4 vectors were correlated against factors hypothesized to be important (directly or indirectly) in determining vegetation change.

The procedure for the multivariate analysis involved first forming a species x sample matrix. This was achieved by calculating the percentage frequency of occurrence in quadrats for all species (57) for each sample (16). The Bray - Curtis measure of dissimilarity with flexible UPGMA clustering was then used to group the samples. There is great difficulty with this type of analysis in recognizing the causes of dynamics which are superimposed on the very strong inertial effects of the system (c.f. van der Valk *et al.* 1994). It was considered that using all species was preferable to the use of only dominant species. Dominant species, particularly those which spread vegetatively, were considered to strongly reflect inertia while transient or secondary species were expected to be more sensitive to (and therefore indicative of) causes of change.

Pairwise Pearson correlations were calculated between vectors and the following factors: (i) relative water's edge, relative water depth (at a single marker point), relative mean elevation (averaged for all quadrats), mean monthly minimum temperature, mean monthly maximum temperature, and maximum species for the sample. Correlations were also performed with a 2 month lag in the above water regime and temperature variables. The significance of correlations was tested with t- tests. The level of significance was reduced to 0.001 using the Bonferroni correction for number of correlations (Section 2.2.2).

(ii) Community dynamics

TWINSPAN analysis was used to generate an initial cluster of quadrats based on floristic similarity along each of the sixteen temporal samples. Three percentage cover groups were used (0, < 10%, ≥ 10%) with default TWINSPAN settings. The stopping rule defining communities was that applied in Section 2.2.2 giving either one, two or three communities for each sample (compare Transect 1 in Appendix 4).

The percentage frequency of occurrence in quadrats was calculated for all species within each of the 39 community transect units identified by TWINSPAN. Cluster analysis (Bray-Curtis with flexible UPGMA) and HMDS ordinations (2-4 vectors) were performed on the resulting 39 'temporal communities' x 57 species matrix. Correlations of ordination vectors with the following floristic and environmental variables were determined: (i) relative mean elevation of the community; (ii) mean monthly minimum temperature; (iii) mean monthly maximum temperature; (iv) species richness; (v) number of wet-dry fluctuations (1993-95) at the transect midpoint of each community; and (vi) inundation index (see Fig. 3.8 for explanation). Correlations were also performed with a two month lag in the first three listed variables. Significance of correlations was tested using t - tests with the level of significance reduced to 0.001 using the Bonferroni correction for number of correlations.

(iii) Species dynamics

Two disparate approaches were explored to describe species dynamics. Initially temporal variation in interspecific association was investigated. Ten visually dominant species were chosen and clustered according to similarity in distribution along Transect 1 for each temporal sample. The binary data (i.e. presence or absence in quadrats) were clustered using an agglomerative technique using average linkage and with group similarity determined by the Jaccard procedure. The question of covariance (independent of the question of association) is the subject of Section 3.4.

Secondly, clustering of temporal samples with similar distributions was carried out for each of the six perennial species included in the direct

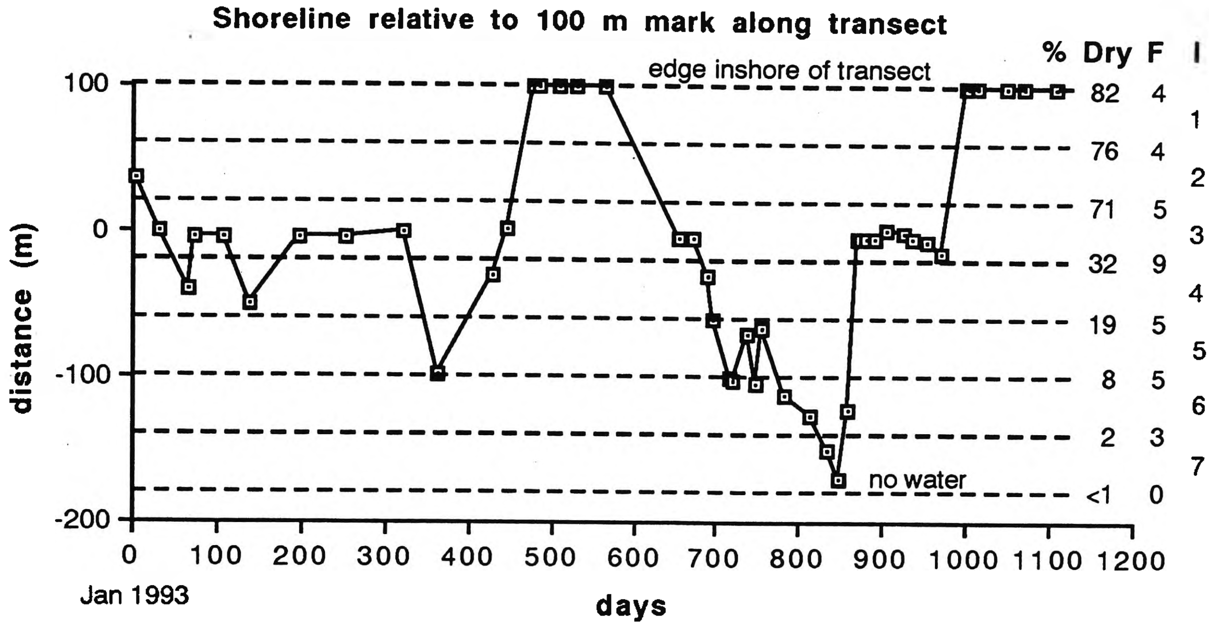


Figure 3.8 The 'inundation index' for Transect 1, a wet meadow - open water transition, at Coomonderry Swamp. The inundation index (I) ranks successive 40 m sections of the transect on the basis of the period of time free from flooding (% dry) and the number of fluctuations from wet to dry (F). Note: the base of the 'dense root' layer, which is about 15 cm below the soil surface (Fig. 4.4), would be in contact with the water table approximately 60 % of the time even at 0 m on the transect.

gradient analysis and a further six species (including some annuals). For each species, the matrix: quadrats with occurrence x temporal samples was initially subjected to Bray-Curtis analysis with flexible UPGMA and HMDS ordination in 1-3 vectors. Correlations were performed and significance tested as previously described in Section 3.3.2.3 part (i). The constancy of the distributions of dominant species masked dynamics as expressed by the similarity coefficient and thus the procedure was repeated focussing on change in abundance by using only occurrences with ≥ 10% cover in quadrats. Significant correlations were compared to trends in the DGA.

3.3.2.4 *Analysis of temporal change along the open-forest - Melaleuca transition*

Direct gradient analysis showing the distribution and abundance of eight visually dominant species was used to compare temporal samples.

3.3.3 Results

3.3.3.1 *Long term vegetation dynamics - broad scale changes and anthropogenic impacts - aerial photographic record*

Generally, forest, open forest, *Melaleuca* scrub and woodland, open water and cultivated and grazed lands were clearly recognized from aerial photographs. Open water areas were more difficult to define when supporting floating plants. Reeds and sedges were difficult to distinguish from each other and, sometimes, from open water. *Typhus orientalis* was light coloured and generally formed sharp boundaries with deep, open water, while sedges were variable, green/brown in shallower areas. Open water with floating vegetation, reeds and sedge could not be clearly distinguished on the black and white photographs.

1949 (1:30000 black & white) (Fig. 3.9) Coomonderry Swamp has changed little in shape and size during the past 50 years (compare Figs. 3.9 & 3.12). Cultivated lands abutted Coomonderry Swamp along the entire western, northern and southern margins much as they do today. Land above the western margin (now grazed) appears to have been used for growing crops. Intergrading areas between dryland and wetland at the southern end of the swamp had been 'reclaimed' by this time. However, the fringe of *Casuarina glauca* - *Melaleuca* spp. - *Eucalyptus robusta* forest, clearly visible along the western margin (still present today) indicates that the wetland edge of the western side was probably well defined when pristine. The main channel, with side arms, is visible running south to north, draining a much greater area of open water than can be seen in later photos. Other notable features include: (i) the extent of Foy's Swamp to the north of Coomonderry Swamp, (ii) the swamp - forest - dunal system was not yet dissected by a road, and (iii) the forested areas to the northwest were more extensive than they are today.

1961 (1:40000 black & white) (Fig. 3.10) Drainage lines were distinct in this photo. Areas of open water (with and without floating vegetation) were larger than they are today, particularly at the northern end of the wetland, but were much reduced, in comparison to 1949, through the central and eastern portions. The distribution of open water patches in 1961 resembles that visible in the 1993 aerial photograph.

At the southern end, a drainage channel clearly divides open water and a drained area. This division is no longer obvious. Areas under cultivation in the catchment to the north and south of Coomonderry were much greater than evidenced in 1949. In particular some region of forest on the hills above Coomonderry Swamp had been cleared. Stands of major vegetation types within the wetland appear similar to the present.

Figure 3.9 Coomonderry Swamp 1949 aerial photograph.

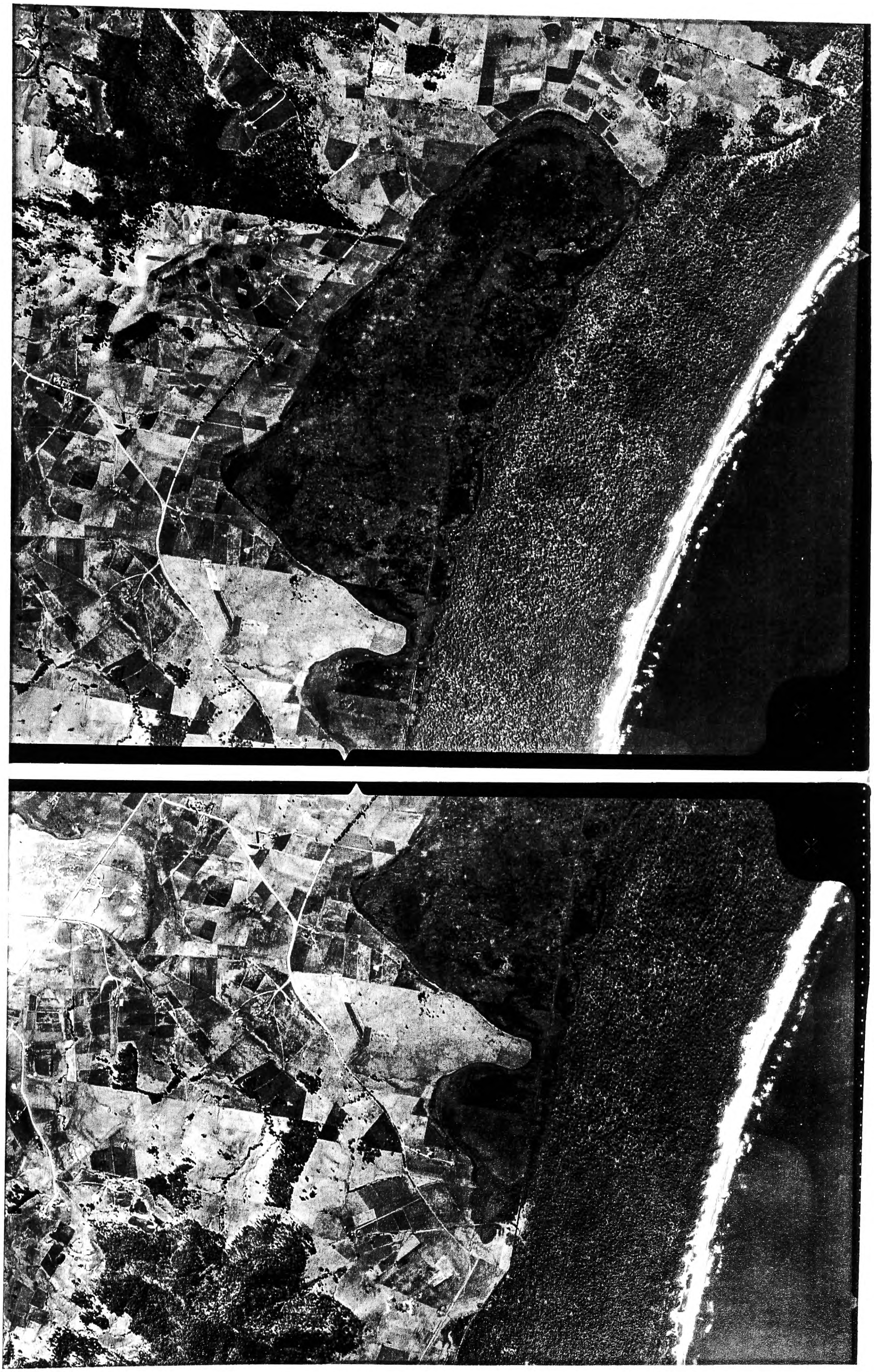


Figure 3.10 Coamonderry Swamp 1961.

1972 (1:20710 colour) Herbaceous vegetation features were not well defined in this aerial photo although the lighter colour along the western interior possibly indicate large stands of *Typhus orientalis.* Open water areas were larger than in the present and, at the time of this photo, appear mostly covered with floating vegetation. Distributions of forest and *Melaleuca* scrub were discernable. In this colour photo *Melaleuca* clumps in the wetland interior were the same as in the present. Boundaries of open water to the south were defined by drainage channels and the 'undisturbed' eastern margin, dominated by *Eucalyptus robusta* could be distinguished.

1981 (1:25000 colour - NSW coastal wetlands) (Fig. 3.11) This aerial photo formed part of the wetland inventory described by Adam *et al.* (1985). Drainage channels and their effect on water flow at the southern end can be clearly seen. At that time, a number of boundaries within the wetland, and across to the eastern shore were fenced (pers. obs.). Land to the west was still under cultivation.

Distributions of major communities in 1981 differed little from the present (Figs. 3.12 & 2.1). Unvegetated open water areas were extensive, but followed a month (May 1981) with above average rainfall. *Typhus,* or perhaps *Phragmites,* adjacent to open water can be seen in the northwest corner and can be contrasted with the amorphous green - browns of *Baumea* species. The wet meadow area at the extreme southern end of the wetland, where much of the work on plant dynamics presented in this chapter was carried out, is clearly visible. Here also land was cultivated close to the wetland margin and the drain dissecting the wet meadow can be recognized.

1986 (1:25000 colour - NSW coastal wetlands) Drainage lines were still clearly visible in this photograph. There were few areas of open water which did not support floating vegetation.

Figure 3.11 Coomonderry Swamp 1981.

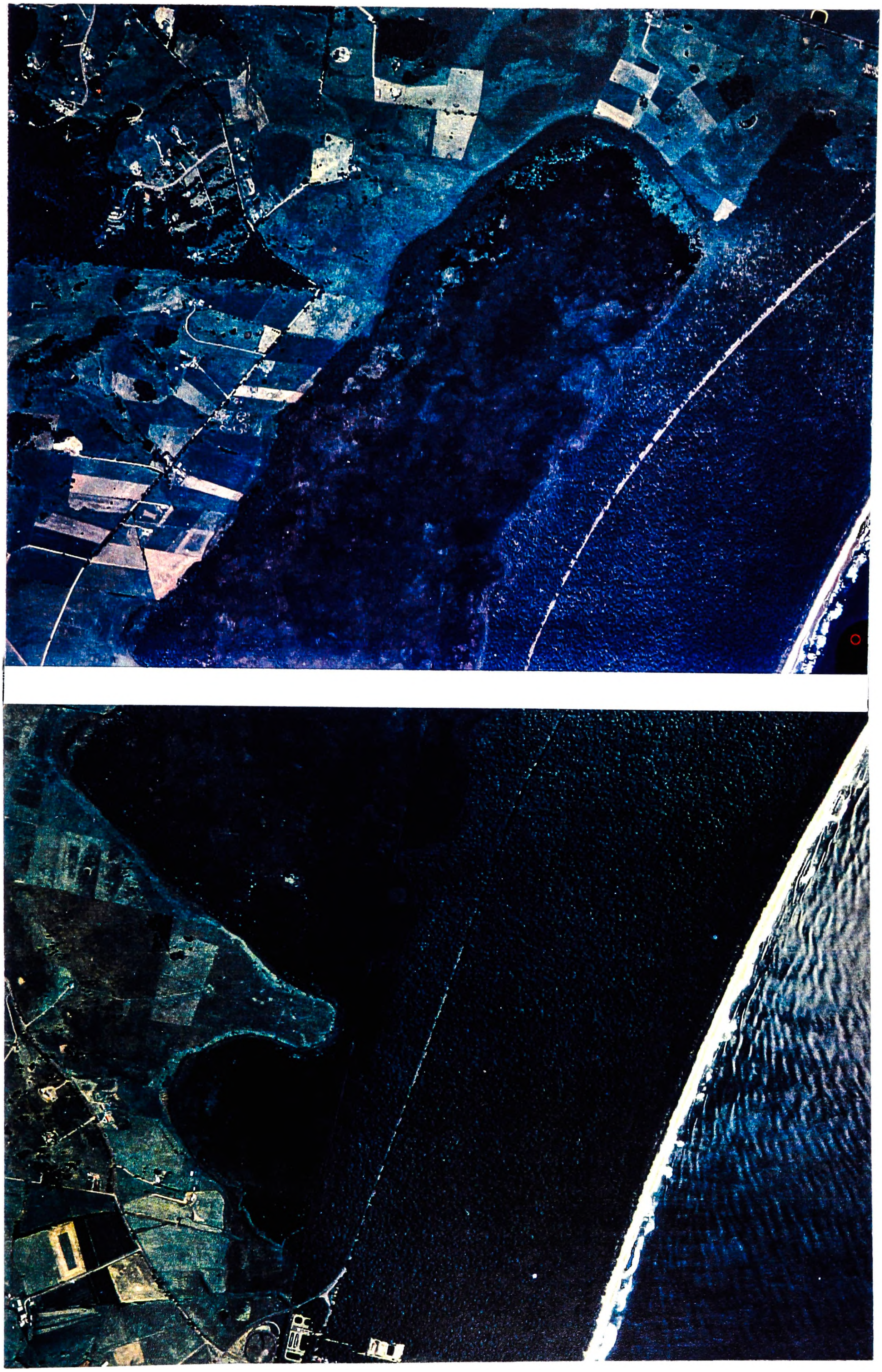


Figure 3.12 Coomonderry Swamp 1993 aerial photographs (reproduced with permission).

1993 (1:25000 colour - coastal surveillance) (Fig. 3.12) This aerial photo coincided with the beginning of the plant community survey reported in Chapter 2. Open water areas were greater in early 1993 (following good rain) than they have been up to 1996. The photo indicates the abandonment of cultivation immediately adjacent to the wet meadow area at the southern part of Coomonderry Swamp and also the turf farm on slightly higher ground.

3.3.3.2 *Short term vegetation dynamics of the wet meadow transition*

(i) Whole transition dynamics

Direct gradient analysis The DGA (Fig. 3.13) illustrated the constancy of the vegetation within wet meadow over the period of survey, irrespective of seasonal change and large variations in inundation levels (Fig. 3.3). Changes in distribution and abundance of individual species are discussed in detail in Section 3.3.3.2, part (iii), however it should be noted from the DGA and the photographic record (Figs. 3.9 - 3.12) that structure was often dictated by the presence (or absence) of three species; over the first 150 m by *Isolepis prolifera* (an introduced species) and *Pseudoraphis paradoxa*, and over the final 70 m of the transect by *Marsilea mutica*. The DGA illustrates only six of the most prolific species and these are all comparativly long-lived, stoloniferous or rhizomatous perennials. While greater variation was shown in the distributions of secondary perennials and annuals, it is obviously more difficult to interpret the causes for dynamics in these species because of their transience (see Section 3.3.3.2, part iii). In particular, the DGA did not indicate the marked changes in species composition and structure at lower elevations (i.e. beyond 200 m) accompanying drawdown and reflooding.

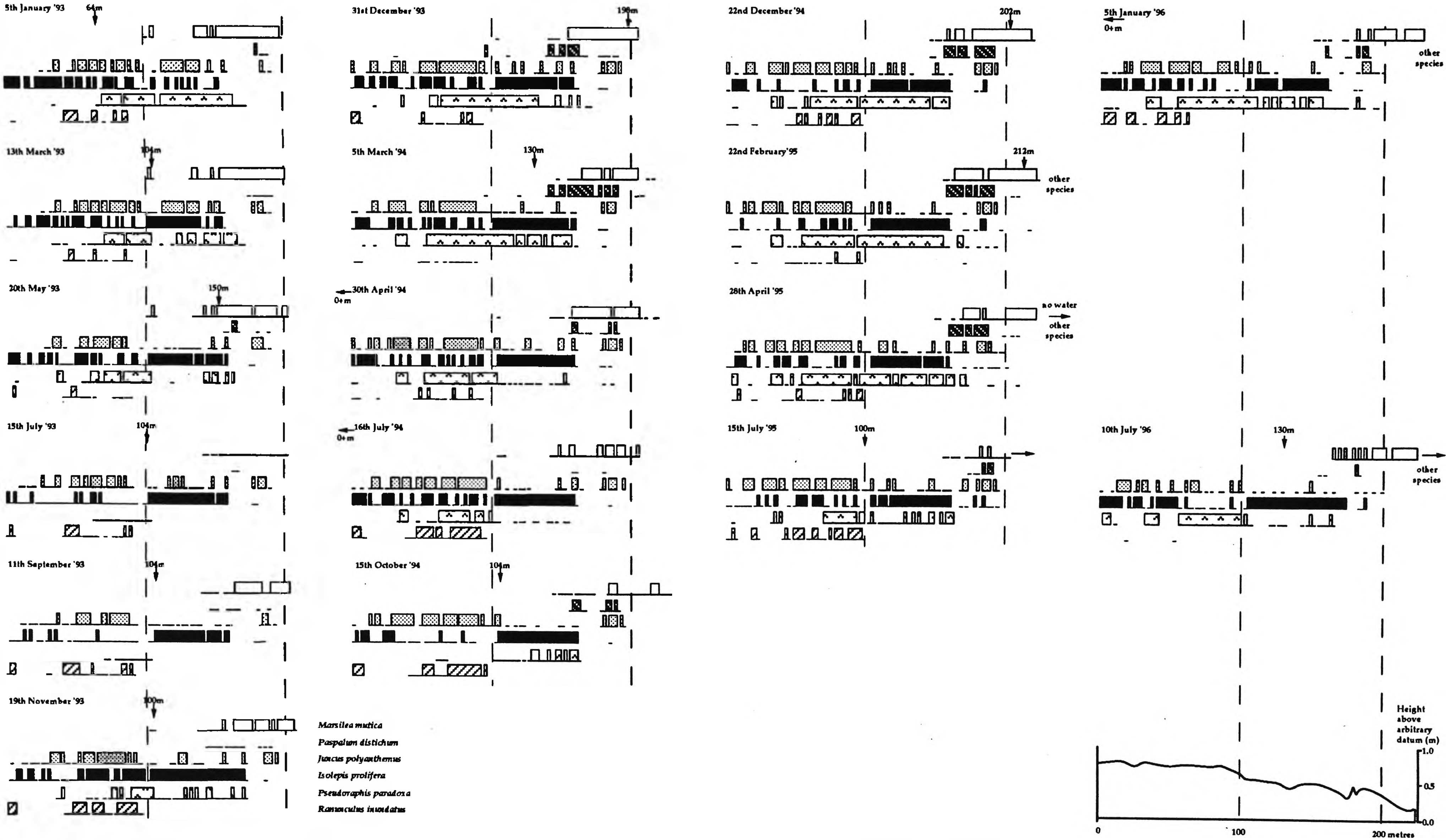


Figure 3.13 Distributions of six perennial plant species along a transect in a wet meadow at Coomonderry Swamp. Lines indicate presence of named species. Shaded areas show % cover ≥ ten. Vertical arrows show water's edge. In April and July 1994, and January 1996, water covered the whole transect. Open water occurred beyond the *Marsilea mutica* except where indicated (i.e. where *Marsilea mutica*, other species or mud continued further down the elevation gradient).

Photographic record The most striking illustration of vegetation dynamics was portrayed in the photographic record (Figs. 3.14 - 3.17). The following observations are important:

(i) There were few gaps in the vegetation canopy over the upper 150 m of the transect in summer (Figs 3.14a &3.16a), however some gaps occurred in winter, particularly when dry, with senescence of the dominant species (*Persicaria* spp. in Fig. 3.17a). These gaps were usually occupied by annuals e.g. *Bidens tripartita* (Fig. 3.15a-c) till later refilled by the vegetatively spreading perennials (e.g. Fig. 3.17b).

(ii) Visually, there was a spatially and temporally distinct boundary at 104 m which indicated a shift in the dominance of two key species; from *Pseudoraphis paradoxa* to *Isolepis prolifera* (Figs. 3.14b & 3.17b). The boundary coincided with the modal water level (Fig. 3.3). Only for one temporal sample did this visual boundary equate with a division of communities defined by cluster analysis (Section. 3.3.3.2, part ii). Interestingly, this cluster analysis division occurred for the October 1994 sample, when both species most closely overlapped in distribution below 100 m, and both were most poorly represented higher on the gradient (Fig. 3.13).

(iii) A second visually distinct boundary i.e. between *Isolepis prolifera* and *Marsilea mutica* was not illustrated in the sequence of photographs. In contrast to the last example, this boundary invariably corresponded to the major cluster division separating wet meadow from the deep water community for each temporal sample (Section 3.3.3.2, part ii). The cluster division consistently occurred, despite a lateral shift of 20 m in these species over the period of survey (Fig. 3.13), and identified a boundary where a range of emergent, inundation-tolerant species (represented by

A

B

Figure 3.14 The wet meadow transition at Coomonderry Swamp in January 1995 (dry summer, following a wet winter) looking north along the elevation gradient. 'A' at 0 m on the transect; 'B' at 100 m on the transect. ...cont'd

C

D

Figure 3.14 (cont'd) The wet meadow transition at Coomonderry Swamp in January 1995 (dry summer following a wet winter). 'C' at 160 m on the transect looking north along the elevation gradient; 'D' at 180 m on the transect looking north-west.

A

B

Figure 3.15 The wet meadow transition at Coomonderry Swamp in April 1995 (very dry autumn following a dry summer) looking north along the elevation gradient. '**A**' at 0 m on the transect; '**B**' at 100 m on the transect. ...**cont'd**

C

D

Figure 3.15 (cont'd) The wet meadow transition at Coomonderry Swamp in April 1995 (very dry autumn following a dry summer). 'C' at 160 m on the transect looking north along the elevation gradient; 'D' at 180 m on the transect looking north-east.

A

B

Figure 3.16 The wet meadow transition at Coomonderry Swamp in January 1996 (very wet summer following a moderately wet winter) looking north along the elevation gradient. 'A' at 0 m on the transect; 'B' at 100 m on the transect. ...cont'd

C

Figure 3.16 (cont'd) The wet meadow transition at Coomonderry Swamp in January 1996 (very wet summer following a moderately wet winter). 'C' at 180 m on the transect looking north-west.

A

B

Figure 3.17 The wet meadow transition at Coomonderry Swamp in July 1996 (moderately dry winter following a wet summer) looking north along the elevation gradient. 'A' at 0 m on the transect; '**B**' at 100 m on the transect. ...cont'd

C

D

Figure 3.17 (cont'd) The wet meadow transition at Coomonderry Swamp in July 1996 (moderately dry winter following a wet summer). 'C' at 160 m on the transect looking north along the elevation gradient; 'D' at 180 m on the transect looking north-west.

Isolepis prolifera) were replaced by a range of truly aquatic, attached or floating species (represented by *Marsilea mutica*).

(iv) Mud exposed during drawdowns (Fig. 3.15d) was quickly covered by a range of ephemeral species (Fig. 2.7). The region beyond 200m, covered by open water with few species during 1993 (Fig. 3.13) experienced a brief drawdown in December 1993 which resulted in a temporary growth of *Persicaria lapathifolia* and *Echinochloa crus-galli* (Fig. 2.8). These species did not persist on immersion. A more extreme drawdown during December 1994 - April 1995 resulted in a stand of the emergent, *Philydrum lanuginosum* (Fig. 3.15d) which has been resilient to subsequent water level changes (Fig. 3.17c & d). *Philydrum lanuginosum* established late in the drawdown.

(v) At lower elevations in Coomonderry Swamp (e.g. at 300 m on Transect 1) tall emergents such as *Typhus orientalis, Baumea articulata* and *Eleocharis sphacelata* have persisted for the duration of record (Figs. 3.14d, 3.15d, 3.16c & 3.17d). The remains of plant stems in the mud at the lowest elevations (Fig. 3.15d) suggested that even these taller species do not tolerate all inundation events.

Cluster analysis Temporal transect samples were not strongly separated by cluster analysis. Five divisions are indicated by the dendrogram (Fig. 3.18), but the ordering was strongly influenced by the inherent similarity of adjacent time units. Thus early divisions generally separated 1993, 1994-95 and 1996 samples. The only indication of abiotic influence was evident in the division of the 3rd and 4th clusters. The 3rd cluster contained samples with some annuals common to the upper meadow as well as floating species, while the 4th division clustered 'dry' temporal samples on the basis of ephemeral annuals found on exposed mud.

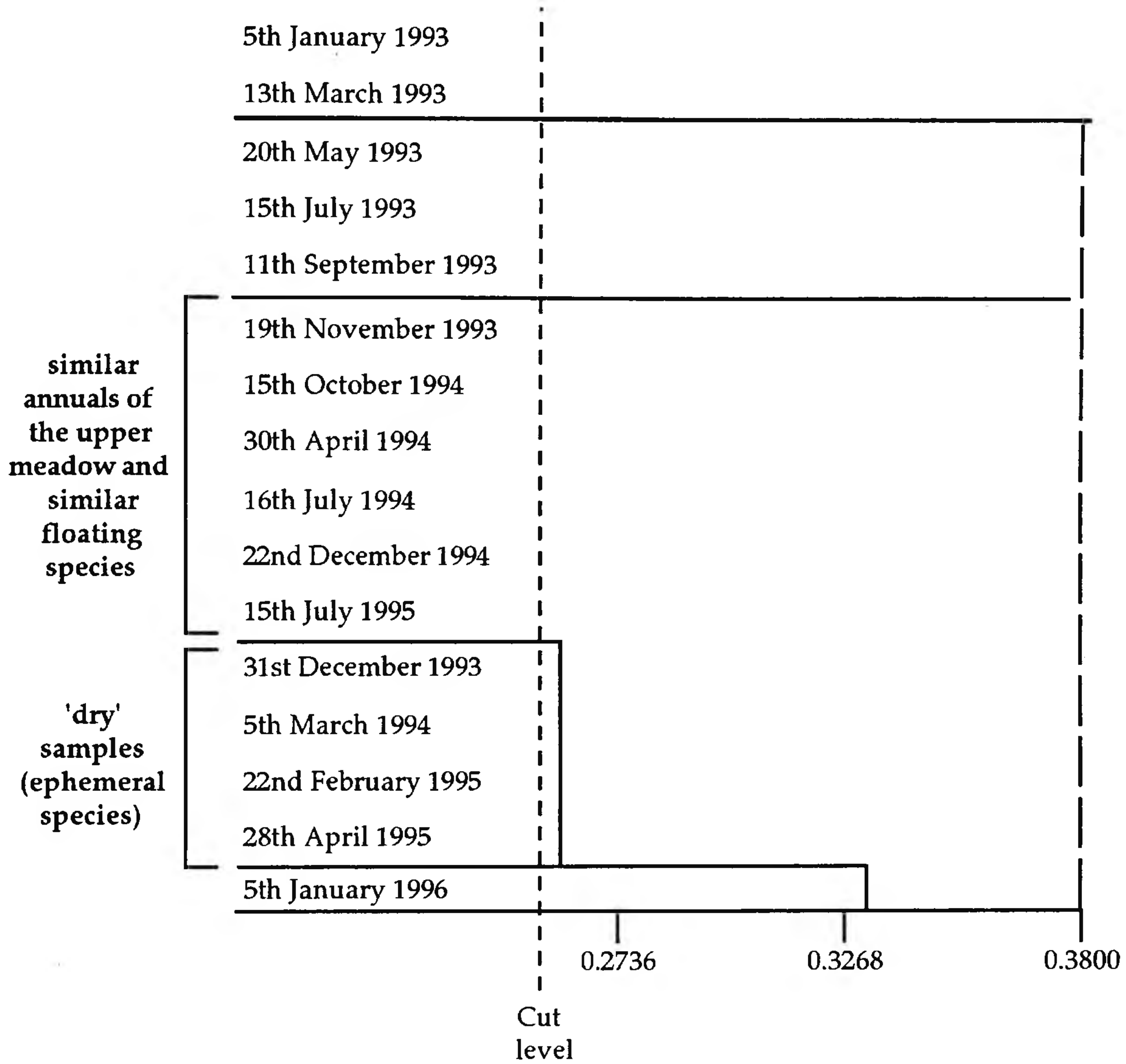


Figure 3.18 Dendrogram derived from cluster analysis of 16 temporal samples of Transect 1, a wet meadow transition at Coomonderry Swamp. Association values are shown along the bottom.

Ordination Though not significant at the 0.001 level, correlations with three ordination vectors suggested some influence of inundation regime, season (and perhaps species interactions) in determining floristics (Table 3.1). Vector 1 showed greatest correlation with a two month lag in inundation characteristics (depth and edge). Vector 2 correlated most strongly with temperature and maximum species. Vector 3 correlated most with maximum species. The maximum number of species was significantly correlated with water depth, being greater during drawdown and least at greatest inundation. This correlation did not persist strongly with two months lag-time.

(ii) Community dynamics There were six predominant groups defined by the cluster analysis of communities (Fig. 3.19). Appendix 8 shows species categories defining each of the clusters. The first division clustered all temporal community samples of the upper elevation as a single, very homogeneous group (Group 1, Fig. 3.19), irrespective of season or inundation flux. Group 1 was termed 'wet meadow' in Chapter 2. Greater vegetation dynamics were exhibited lower on the elevation gradient with samples clustered into five groups. Groups 2 and 3 represented deep freshwater communities (as defined in Ch. 2). Group 2 included only spring - summer samples dominated by *Marsilea mutica, Azolla filiculoides, Spirodella punctata* and *Pseudoraphis paradoxa*. Group 3 samples shared *Marsilea mutica* as the dominant component (two exposed mud samples - December 1994 and April 1995 - were clustered in this group due to the strong presence of this species). Group 4 contained only one sample, the lowest elevation, 'ephemal mud' community of April 1995. This community still retained remnant *Marsilea mutica*. Group 5 communities represented the ephemeral mud - deep freshwater temporal transition having both remnant, flood intolerant species and truly aquatic species.

Table 3.1 Pearson correlations of three vector ordination of temporal change in plant species composition along the wet meadow transition at Coomonderry Swamp with maximum species and inundation and temperature variables.

	Vector 1	Vector 2	Vector 3	relative water's edge	relative water depth	relative mean elevation	mean m. minimum temp.	mean m. maximum temp.	maximum species	2 month lag rel. edge	2 month lag rel. depth	2 month lag rel. elevation	2 month lag mean m. min. temp.
relative water's edge	-0.319	-0.458	0.098										
relative water depth	0.426	0.469	-0.238	**-0.965***									
relative mean elevation	-0.373	-0.470	0.104	**0.982***	**-0.975***								
mean monthly min. temp.	0.302	-0.614	0.036	0.102	-0.127	0.088							
mean monthly max. temp.	0.283	-0.657	0.145	0.222	-0.251	0.197	**0.949***						
maximum species	-0.262	-0.642	0.404	0.709	**-0.801***	0.738	0.295	0.353					
2 month lag rel. edge	-0.482	-0.195	0.100	0.523	-0.514	0.536	-0.155	-0.200	0.542				
2 month lag rel. depth	0.508	0.126	-0.280	-0.479	0.498	-0.506	0.278	0.293	-0.557	**-0.963***			
2 month lag rel. mean elev.	-0.492	-0.071	0.170	0.457	-0.456	0.471	-0.288	-0.319	0.491	**0.981***	**-0.975***		
2 m. lag mean m. min. temp.	-0.326	-0.478	-0.042	0.102	-0.183	0.203	0.384	0.267	0.336	0.207	-0.189	-0.288	
2 m. lag mean m. max. temp.	-0.426	-0.575	0.150	0.262	-0.359	0.339	0.396	0.290	0.532	0.296	-0.293	-0.319	**0.934***

Critical value: $P = 0.001$. $*P < 0.001$. See text for description of variables. 'n' = 16 temporal transect samples.

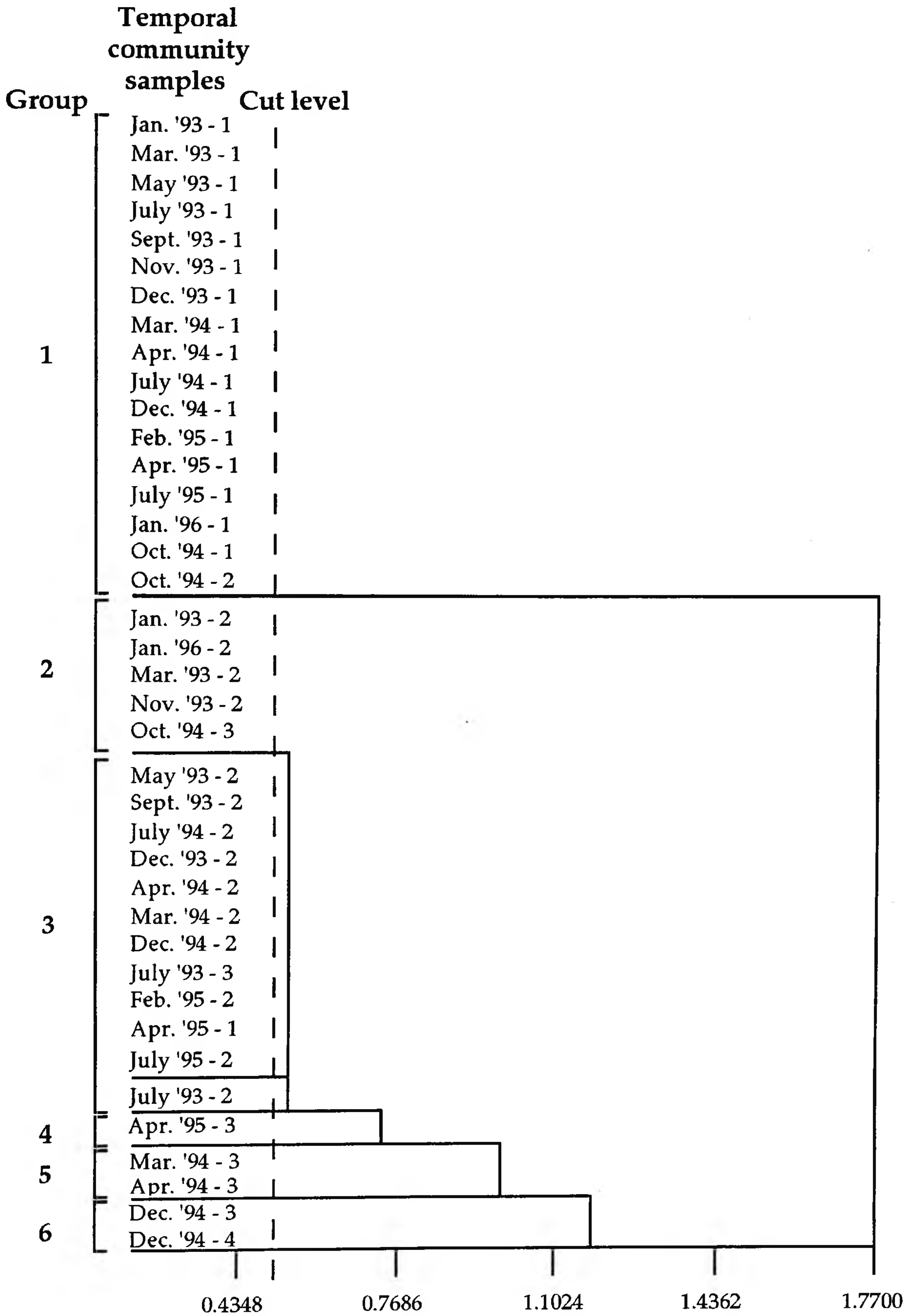


Figure 3.19 Dendrogram derived from cluster analysis of 39 temporal samples of the communities along the wet meadow transition at Coomonderry Swamp. Communities from each sampling event are named 1 - 4 down the elevation gradient.

Group 6 defined an ephemeral community of *Saggitaria graminea* established at the lower end of the transect during the December 1994 drawdown. *Saggitaria graminea* was later displaced by the resilient emergent *Philydrum lanuginosum* (Fig. 3.17c & d).

Four vector ordination gave the best indication of possible factors important in differentiating floristics at the community level. Vector 1 correlated very strongly with inundation index (r = 0.951), which in turn was negatively correlated with both species richness and relative mean elevation (Table 3.2). The inundation index summarized relatively long term inundation change and thus was more likely to show an influence on floristics than other inundation variables which reflected immediate or recent change in water levels only. Vector 2 correlated significantly with two month lag in mean maximum temperature and vector 4 with the number of wet-dry fluctuations. None of the measured variables correlated well with vector 3.

(iii) Species dynamics

Interspecific association Temporal changes in pairwise species associations were illustrated by combining dendrograms with shade diagrams (Fig. 3.20). The three examples chosen for display once again indicate the constancy in species distributions through time and the strong inertia of the system. Thus July 1994 and Dec. 1994 samples (with disparate inundation and season) are more similar than Dec. 1993 and Dec. 1994 (with similar lead-up conditions, inundation and season). A number of additional observations may be drawn from Fig. 3.20: (i) the order of species listed reflected changing distributions down the elevation gradient (compare Fig. 3.13); (ii) this order showed only small change through time for dominant species; (iii) species richness (realized niche overlap) was much greater at the upper part of the

Table 3.2 Pearson correlations of four vector ordination of temporal change in plant species composition within community transect units along the wet meadow transition at Coomonderry Swamp with species richness and inundation and temperature variables.

	Vector 1	Vector 2	Vector 3	Vector 4	relative mean elevation	number wet - dry cycles	inund. index	mean m. minimum temp.	mean m. maximum temp.	species richness	2 month lag rel. elevation	2 month lag mean m. min. temp.
relative mean elevation	**-0.514***	0.117	0.390	-0.094								
number of wet-dry cycles	0.260	0.373	-0.357	**0.593***	-0.351							
inundation index	**0.951***	-0.091	-0.299	0.205	**-0.533***	0.297						
mean monthly min. temp.	0.024	-0.497	0.160	0.063	0.043	-0.089	-0.001					
mean monthly max. temp.	0.023	-0.464	0.228	-0.010	0.129	-0.123	0.010	**0.938***				
species richness	**-0.686***	-0.459	0.077	-0.018	0.465	-0.348	**-0.595***	0.194	0.168			
2 month lag rel. mean elev.	-0.477	0.109	0.328	-0.131	**0.652***	-0.394	-0.476	-0.151	-0.205	0.459		
2 m. lag mean m. min. temp.	0.051	-0.446	-0.063	0.151	0.010	-0.160	0.062	0.325	-0.187	0.279	0.308	
2 m. lag mean m. max. temp.	0.157	**-0.533***	0.064	0.073	0.063	-0.229	0.130	0.468	0.353	0.247	0.247	**0.911***

Critical value: $P = 0.001$. $^*P < 0.001$. See text for description of variables. 'n' = 39 temporal samples of communities.

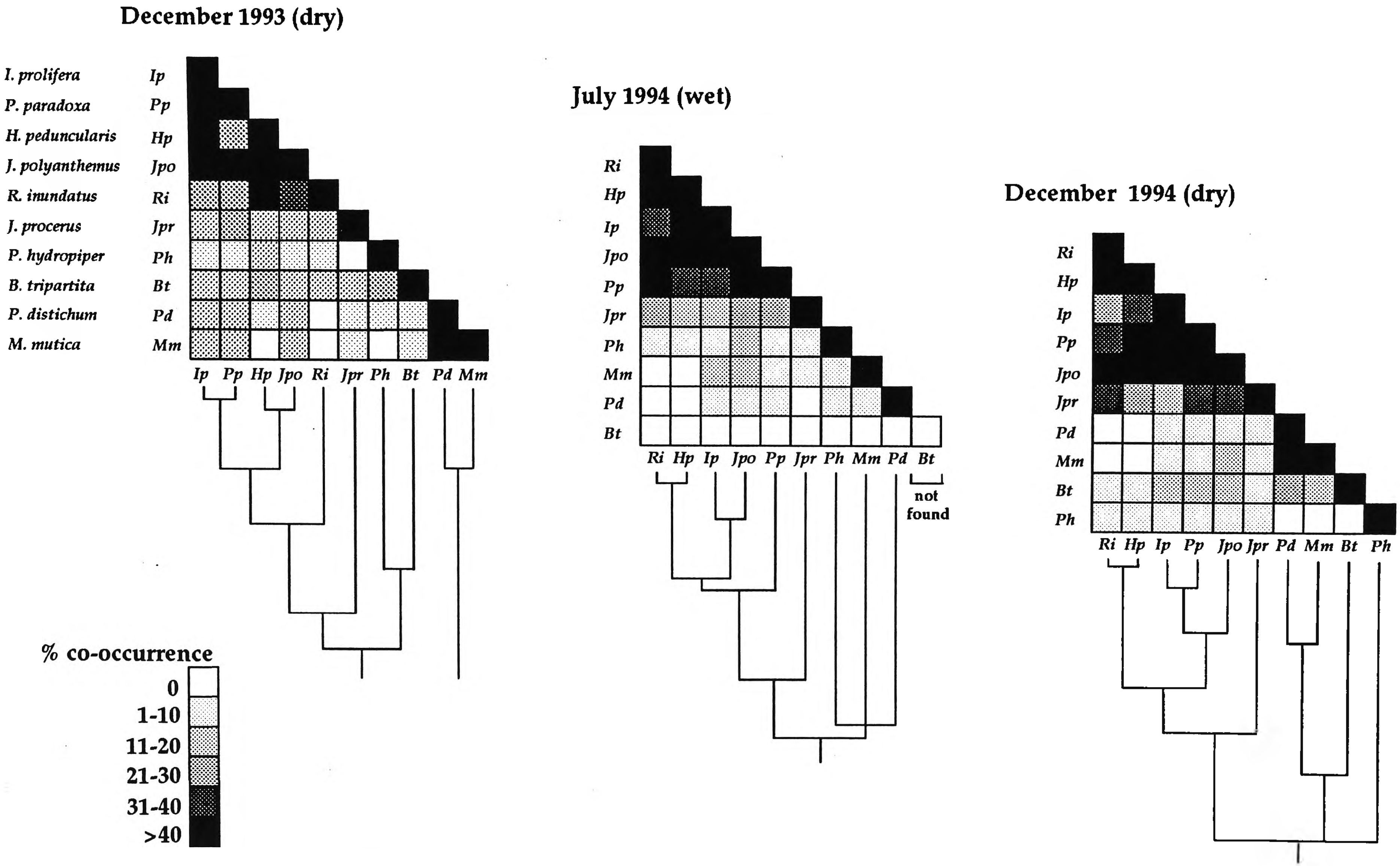


Figure 3.20 Shade diagrams and dendrograms derived from cluster analysis of the pairwise co-occurrences of ten species along the wet meadow transition at Transect 1, Coomonderry Swamp on three occasions: December 1993, July 1994 and December 1994.

transect; and (iv) dry conditions were marked by increased species richness at lower elevations. For example *Bidens tripartita* and *Persicaria hydropiper* normally restricted to gaps at upper elevations, flourished at lower elevations during drawdown.

Cluster analysis and ordination of temporal samples of species' distributions
Cluster analysis and ordination poorly separated temporal samples of the distributions of individual species. However, while not strong, the pattern analyses were able to be confirmed by corresponding trends in the DGA (Fig. 3.13). These comparisons are presented in Tables 3.3 & 3.4, while cluster analyses and ordinations for each species are shown in Appendix 9. DGA's for the six species not shown in Fig. 3.13 are available on request from the author.

3.3.3.3 *Short term vegetation dynamics of the Open-forest - Melaleuca transition*

Direct gradient analysis showed little evidence of change in the distribution and abundance of dominant woody and herbaceous terrestrial species along the undisturbed, open-forest - *Melaleuca* transition at Coomonderry Swamp (Fig. 3.21). The vegetation and terrain were not easy to negotiate, and canopy cover was difficult to assess. Small variations among temporal samples could well be the result of inaccurate estimates of cover. Changes were more obvious in herbaceous species of the water margin and *Melaleuca ericifolia* understory, however the continuous presence of *Azolla filiculoides* and other aquatic species contrasted with their more transient occurrence in open waters of the wet meadow transition.

Table 3.3 A comparison of direct gradient analysis, cluster analysis and ordination of temporal samples for 'dominant' species along the wet meadow transition at Coomonderry Swamp

Species	Direct Gradient Analysis	Cluster Analysis	Correlation with ordination vectors
Isolepis prolifera	0 - 190 m. Most abundant during wet spring-summers following dry winters. Most dominant species over 100 - 150m irrespective of season or inundation. Hence seasonal decline not apparent in Fig. 3.11.	No clear separations.	3 vectors: V1: greatest correlation with max. species: r = -0.713, $P < 0.005$, but also temperature; V2: weak negative corr. with lag in temperature; V3: some corr. with lag in inundation factors.
Pseudoraphis paradoxa	0 - 200 m. Very constant distribution. Strong summer growth. Greatest decline in abundance winter - autumn at 100 - 150m i.e. where *Isolepis prolifera* is most dominant.	4 clusters: (i) abundant 30 - 170m (summer-autumn) (ii) abundant 30 - 100m (autumn-spring) (iii) abundance < 10% all quadrats (winter) (iv) mixed group?	2 vector: V1: greatest correlation with lag in mean max. temp: r = -0.666, $P < 0.005$; V2: correlated most with mean max. temp.
Juncus polyanthemus	0 - 200 m. Constant distribution. Some abundance decrease in winter-spring at 100 - 150m not shown by DGA.	No clear clusters	Correlations weak
Juncus procerus	60 - 190 m. Constant and resilient species	Cluster closely follows temporal sequence.	Correlations weak
Paspalum distichum	150 - 190 m. Narrow distribution. Winter decline. Some increase in abundance and distribution in dry conditions.	No clear clusters	3 vectors: V1: greatest correlation with depth: r = -0.596, $P < 0.02$; V2: weak correlations; V3: some corr. with max. temp.
Marsilea mutica	0 - 250 m. Strong winter-spring reduction, but less in July '96. Shift in distribution down gradient over time	Good distinction of summer-autumn high abundances from winter-early spring low abundances.	3 vectors, all weak: V1: mean relative elevation; V2: lag in water's edge V3: temperature.

Range over 3.5 years of study given for each species. 'n' temporal samples = 16. Correlated variables are explained in the text Section. 3.3.2.3 (iii).

Table 3.4 A comparison of direct gradient analysis, cluster analysis and ordination of temporal samples for 'secondary' species along the wet meadow transition at Coomonderry Swamp

Species	Direct Gradient Analysis	Cluster Analysis	Correlation with ordination vectors
Ranunculus inundatus	0 - 100 m. Initially considered a constant and resilient species showing some decline in Autumn, but then showed a greater decline in July '96.	Some division on the basis of distribution size.	1 vector: greatest correlation with maximum species $r = -0.671$, $P < 0.005$.
Hydrocotyle peduncularis	0 - 95 m. Significant winter decline, but also consistent decline Jan - July '96.	Four main clusters based on distribution size and location.	1 vector: greatest correlation with maximum temperature $r = 0.532$, $P < 0.05$.
Agostis avenacea	0 - 75 m. General increase in abundance and distribution over the period of survey.	Cluster closely follows temporal sequence.	No strong correlations.
Persicaria decipiens	0 - 190 m. Broad but sporadic distribution, not abundant. Most abundant in 1993. Greatest decline in winter .	Cluster follows temporal sequence with shift in distribution from upper elevation to lower elevation.	2 vectors: V1: greatest correlation with depth $r = -0.748$, $P < 0.001$; V2: some corr. with factors related to elev. and temperature.
Persicaria praetermissa	0 - 190 m. Not detected till Mar. '94, confusion with *P. decipiens?* Increasing with dry period from Dec. '94. Winter decline.	Reflects increasing distribution as in DGA. Some seasonal separation?	2 vectors: V1: some corr. with mean max. temp. $r = 0.586$, $P < 0.1$ ($n = 9$); V2: best corr. with lag in mean rel. elevation $r = -0.662$, $P < 0.1$.
Bidens tripartita	0 - 210 m. Distribution dependent on gaps, usually dryer ground. Marked responses to season and inundation i.e. gap availability.	Seasonal separation obvious. Separate clusters of dry and wet distributions.	2 vectors: V1: best corr.with water's edge: $r = -0.764$, $P < 0.02$; V2: best corr. with lag in min. temp. $r = -0.663$, $P < 0.05$ ($n = 10$).

Range over 3.5 years given. 'n' temporal samples = 16 unless species did not occur at ≥ 10% cover in any quadrat. Correlated variables are explained in the text Section 3.3.2.3 (iii).

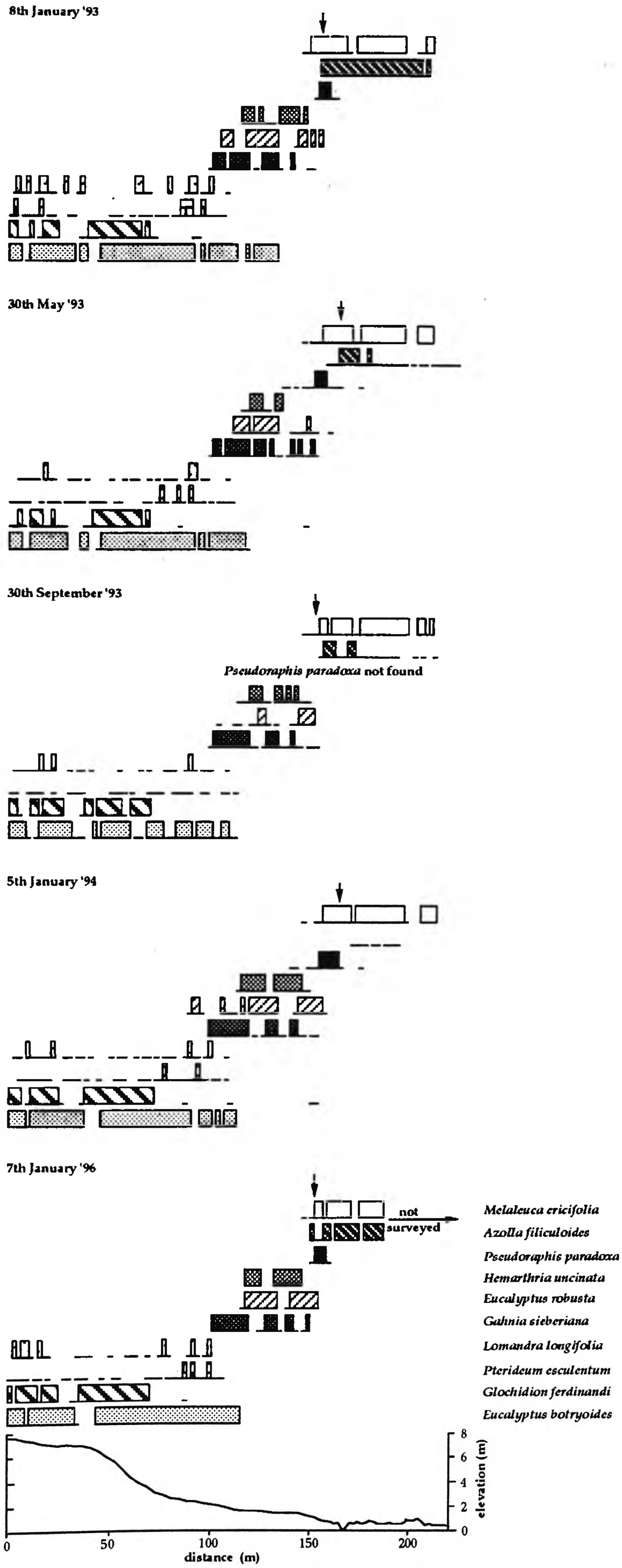


Figure 3.21 Distributions of eight plant species along a transect in undisturbed vegetation at Coomonderry Swamp. Lines indicate presence of named species. Shaded areas show % cover ≥ ten. Arrows show water's edge.

3.3.4 Discussion

3.3.4.1 *Long term vegetation dynamics - broad scale changes and anthropogenic impacts - aerial photographic record*

The 1949 aerial photograph showed intensive land use around Coomonderry Swamp and drainage lines in the wetland. Historical accounts suggest that efforts to drain Coomonderry Swamp and other nearby wetlands were initiated in the early 1800's (Appendix 2). However, in comparison to the Shoalhaven River alluvial plain, where most wetlands have been lost, drainage at Coomonderry Swamp has been unsuccessful. In size and shape, the wetland has not appreciably altered over 50 years. The relatively undisturbed state of the eastern margin is most likely a consequence of: (i) the resilience to draining and impenetrability of the wetland itself; (ii) poor (sandy) farming soils and (iii) poor timber quality. On the other hand, remnant stands of *Eucalyptus robusta, Casuarina glauca* and *Melaleuca* spp. remain the only indicators of pristine structure on the western, southern and northern boundaries.

The long term aerial photographic record confirmed the integrity of major community boundaries defined in Chapter 2 over 50 years. Open water areas showed little change in position, but varied substantially in size and plant cover.

3.3.4.2 *Short term vegetation dynamics of the wet meadow transition*

This discussion focusses on edaphic factors; biotic interactions and their influence in conjunction with abiotic influences are dealt with more completely in Section 3.4.

The various analytical methods used to explore vegetation change along the wet meadow transition did not support the degree of change that was apparent from visual inspection (see Figs. 3.14-3.17). Colour and structural changes in vegetation, and the presence of small gaps at upper levels emphasized by photography, were less significant in comparisons of species occurrence and densities.

On the other hand, direct gradient analysis, cluster analysis and ordination illustrated the constancy of dominant, and even secondary perennial species, and their resilience to change once established. Sequential temporal samples were often clustered together despite seasonal shift or variation in inundation. This was sometimes even the case at lower elevations where disturbance and abiotic stress were most extreme.

Three broad categories of factors were hypothesised to be responsible for floristic variation along the gradient: (i) those related to inundation (including soil responses); (ii) those related to season; and (iii) biotic interactions. A nutrient gradient was not considered to be a significant factor (Table 4.1) but nutrient inputs require monitoring given predicted agricultural impacts on this area of the wetland. It was also beyond the scope of this study to investigate grazing by native mammals, occasional cattle, and wading and feeding by birds. These 'top down' influences could be important and require research.

The analytical methods (discussed below) differed in how they showed the influence of inundation and season in determining floristics: the whole transect ordination (Section 3.3.3.2.i) was important because it showed a significant correlation between the maximum number of species on the transect and inundation variables (but not lag-time in inundation or temperature); community analysis (Section 3.3.3.2.ii) most clearly indicated the difference in dynamics between the upper and lower portions of the elevation gradient; and direct gradient analysis with the species level analyses (Tables 3.3 & 3.4) showed how the importance of inundation and season varied among species.

Whole transect ordination The increase in species with a lowering in the water level suggests that recruitment of herbaceous wetland plants may be geared predominantly to the availability of gaps during drawdowns (which may occur at any time), and that season may not be as important for triggering germination of seeds and other propagules as it is in terrestrial systems. This question of seasonality of recruitment is further explored in Section 4.3. Lack of correlation with lag-time in inundation variables suggests that many early invaders are subsequently competitively excluded.

Community analysis Three important conclusions can be drawn from the community analysis:

(i) The combination of duration, frequency and depth of inundations over a substantial time frame (as described by the inundation index - Fig. 3.8) appeared to be the most important determinant of floristics and structure along the wet meadow transition. Simpler measures, for example, relative depth or elevation, did not correlate well with floristic variation over time. (Establishment from natural seed banks, under varying combinations of flooding depth, duration and frequency has recently been shown to result in diverse plant communities in manipulated experiments - Casanova & Brock 1996).

(ii) The wet meadow community of the upper elevation was relatively stable. Over the period of study it showed little change in distribution, composition or structure. The division of wet meadow into a dryer herb-grass association and at lower elevation, into a Cyperaceae -

Juncaceae subgroup (suggested in Section 3.2.4) was not warranted. Only for one temporal sample (October '94) was this division made by TWINSPAN at the applied stopping level.

(iii) Communities at lower elevations were much more transient than wet meadow. While the deep freshwater community type '*Marsilea* complex' was predominant, at other times 'open water', 'open water plus emergents' and 'ephemeral mud' communities existed.

Species analyses The major conclusions of the species dynamics investigation were:

(i) There were pairs or groups of species which were strongly positively associated e.g. *Pseudoraphis paradoxa* with *Isolepis prolifera,* and *Ranunculus inundatus* with *Hydrocotyle peduncularis* (Fig. 3.20). Positive associations, and hence species richness, decreased down the gradient from more mesic (less disturbance, less edaphic stress) to harsher conditions. (Hypothesized causes for associations and covariances are explored in Section 3.4).

(ii) Some species showed only minor variations in distribution and abundance under the prevailing conditions e.g. *Juncus polyanthemus* and *Juncus procerus.* Species or suites of species occupying a relatively narrow elevation range over an extensive geographic range might prove to be good indicators of wetland boundaries. This potential is further examined in Section 3.5.

(iii) There were species which showed marked seasonal decline. These included *Pseudoraphis paradoxa, Marsilea mutica* and *Bidens tripartita.*

(iv) There was some indication that longer lived, shortly rhizomatous perennials responded less dramatically to inundation fluctuations than quickly spreading perennials or annuals. Species which showed greatest response to the inundation regime included *Paspalum distichum, Marsilea mutica, Persicaria* spp. and *Bidens tripartita.* These species were sometimes well distributed and abundant.

A model of cyclic change Community dynamics at lower elevations corresponded well with the generalized model of van der Valk (1981) (Fig. 3.4) and as well to the precurser of the model i.e. a prairie glacial marsh described by van der Valk and Davis (1978). A model of cyclic change in herbaceous communities at lower elevations at Coomonderry Swamp is illustrated schematically in Fig. 3.22. It is hypothesised that the model describes all possible outcomes under existing variations in conditions.

Wet meadow, is considered to represent a later successional community than the ephemeral mud community (Section 3.4.4). It has developed at slightly higher elevations, under a sustained regime of more moderate variation in inundation (Fig. 3.8). Within wet meadow there was evidence that natural regeneration of woody species was occurring following the cessation of grazing (Section 4.2.3.4). On the other hand, during dry periods, and at the highest elevations, dry meadow species and grasses were establishing. The relationship of wet meadow to the ephemeral mud community, and the alternative successional changes which could potentially occur to wet meadow, are also presented in Fig. 3.22. The relationships between herbaceous communities at Coomonderry Swamp are reviewed in a broader context in Section 5.2.1 as part of an overview of wetland types on the south coast of NSW.

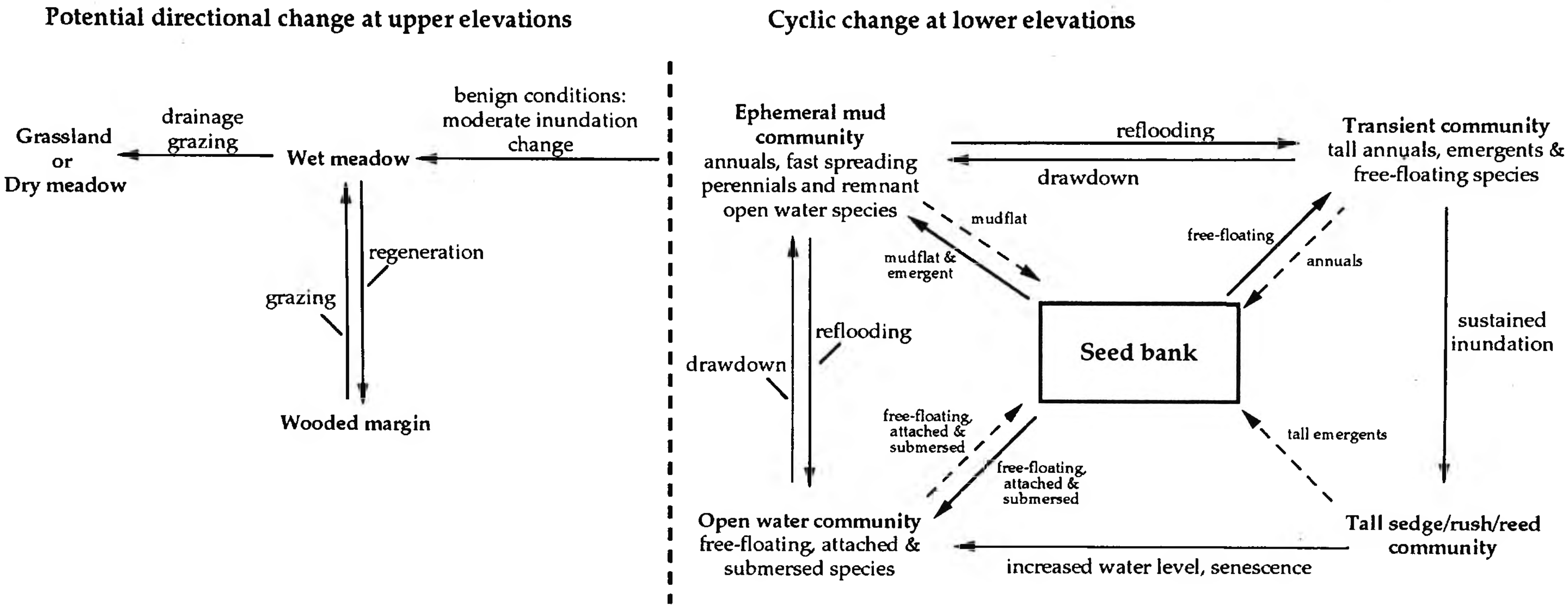


Figure 3.22 A schematic model of potential vegetation change along the wet meadow - open water transition at Coomonderry Swamp. Cyclic change at lower elevations and interactions with the seed bank are shown on the right (follows van der Valk & Davis 1978). Predicted successional changes in wet meadow are shown on the left.

Biotic factors Clearly there were a range of species responses to abiotic change contributing to the dynamics of wet meadow, deep water and ephemeral communities. It needs to be reiterated that the measured responses for most species (and particularly in wet meadow) might be constrained by biotic factors (see Section 3.4). Keddy (1983) made this point when discussing the difficulty of separating ecotonal effects from those of competition on lakeshores. He argued that physical factors may only affect one or two dominants which then competitively induce all other species to respond at the same point on the gradient. Such might well be the case along the wet meadow transition and along other gradients described in Chapter 2. Different sets of conditions and combinations of species could see individual species responses varying greatly. Distributions and abundances of some species among a diverse range of wetland conditions were considered in Chapter 2 and are summarized in Appendices 5 and 6.

3.3.4.3 *Short term vegetation dynamics along the Open-forest - Melaleuca transition*

The lack of short term, annual variation in the composition of woody vegetation along the Open-forest - *Melaleuca* transition was anticipated given the stability suggested by the longer term photographic record. It should be said however, that transect analysis proved to be an inadequate method for estimating canopy dynamics. High resolution remote sensing techniques would be better suited for measuring canopy densities.

Greater seasonal variation was expected to be indicated by the direct gradient analysis in the herbaceous strata of both the open-forest and *Melaleuca* scrub. Repeated seasonal sampling however was beyond the scope of the present study.

There is much yet to learn about the determinants of vegetation change at the 'terrestrial - aquatic' ecotone of the undisturbed, wooded margin. Keddy (1983) considered that shoreline assemblages of lakes in Ontario were indirectly controlled by physical factors constraining the lower limits of 'terrestrial' shrubs. However, undisturbed wetland margins on the south coast of NSW may be very different to the shores of Canadian lakes. At some places along the wooded margin at Coomonderry Swamp, and at other wetlands, typically wetland plants such as *Melaleuca ericifolia* and various Cyperaceae were found growing well above the existing shoreline. At other places, typically terrestrial plants grew to the water's edge. Some of these variations in the terrestrial distribution of wetland species may relate to differences in the gradation of soils (from humic to sandy) along the elevation gradient, but more research is needed.

3.4 The role of biotic factors in determining zonations at Coomonderry Swamp

3.4.1 Aim

To examine plant interspecific covariances (i.e. pairwise comparisons of changes in abundance). Do they vary through time? Do they vary along the gradient from mesic to harsh conditions?

3.4.2 Method

The ten temporal data sets (December 1993 to January 1996) were composed of percentage cover estimates (to the nearest 10%) for all species in contiguous quadrats along the wet meadow transition (Section 3.3.2.2). Pairwise species comparisons using Pearson correlations were performed for each of these temporal samples, and for a range of reasons, a significance level of 0.001 was used. There is an assumption of normality with the use of

Pearson correlations. However multiple comparisons on large data sets were much more easily performed using the procedure, and so it was carried out in preference to the Spearman Rank coefficient. A further difficulty was the prevalence of double zeros (a problem common to vegetation data - Ludwig & Reynolds 1988). Double zeros are laborious to extract from multiple, large data sets and thus the problem was partly avoided by examining a subset of comparisons where pairs of species broadly overlapped (Ludwig & Reynolds 1988). For the present data sets, both double zeros and the Spearman Rank coefficient more commonly resulted in a systematic bias towards positive correlations (Fig. 3.23h). Although where there is no species overlap or overlap is minimal, correlations will be negative (e.g. Fig. 3.23k).

A final problem lies in the identification of pairwise interactions in a multispecies system. Species are not independent and thus neither are statistical tests. However all these problems are ameliorated to a degree because the temporal samples constitute a set of ten replicates. Nevertheless, hypotheses concerning the nature of interactions need to be further tested in manipulated experiments.

3.4.3 <u>Results</u>

Most pairwise correlations for each temporal data set for the wet meadow transition were negative (i.e. 76% ± 1% of correlations were negative; n = 10 temporal samples with between 27 and 41 species), despite the bias towards positive correlation values engendered by the presence of double zeros. There were more negative correlations during drawdowns when there were more species on the transect (i.e. the proportion of negative correlations itself correlated strongly with maximum species number: $r = 0.76$, $P < 0.02$).

Temporal shifts in pairwise covariances for seven species found along the wet meadow transition are shown in Fig. 3.23. Also presented are pairwise covariances for two floating species with *Marsilea mutica*. However, these floating species were not present at all sampling times. The following observations are important:

(i) Correlations were negative where species co-occurrences were low i.e. Fig. 3.23e,k,o,r,s,t and v.

(ii) Most correlations of co-occurring species with *Isolepis prolifera* were negative i.e. Fig. 3.23a,b,c and d (but see Fig. 3.23f). *Isolepis prolifera* was the dominant species of the upper - mid portion of the transition.

(iii) Correlations between broadly overlapping species pairs of the upper - mid transition were generally positive i.e. Fig. 3.23g,i,j,l,m,n,q and u.

(iv) At lower elevations, where species co-occurred, correlations were positive i.e. Fig. 3.23w and x.

(v) Most correlations between species pairs were relatively constant over time. Only a few pairs showed marked temporal fluctuations in covariance i.e. Fig. 3.23c,f,p and x.

3.4.4 Discussion

The large proportion of negative correlations for each temporal sample is considered to primarily reflect niche differentiation (i.e. limited or no pairwise overlap), and secondarily, to reflect competition where overlap was more substantial. The proportions of negative pairwise correlations increased during drawdowns because 'new' species establishing on exposed mud had limited distributions and because some existing species suffered die-back under these conditions (pers. obs.).

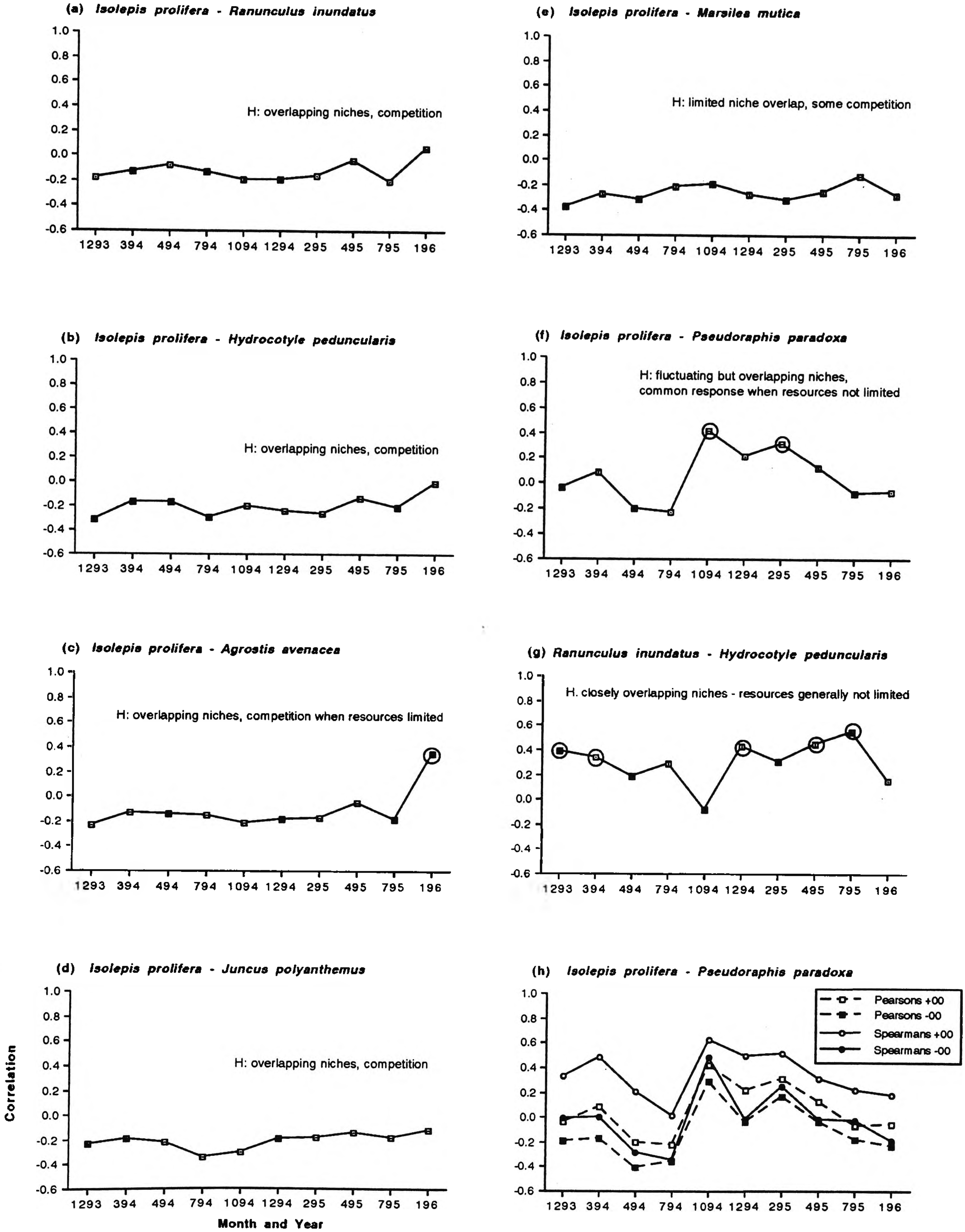


Figure 3.23 Changes in species pairwise covariances over two years along the wet meadow transition at Coomonderry Swamp. Significant Pearson correlations are circled (but see Section 3.4.2). Hypotheses are suggested regarding the causes for observed temporal changes in covariances. **...cont'd**

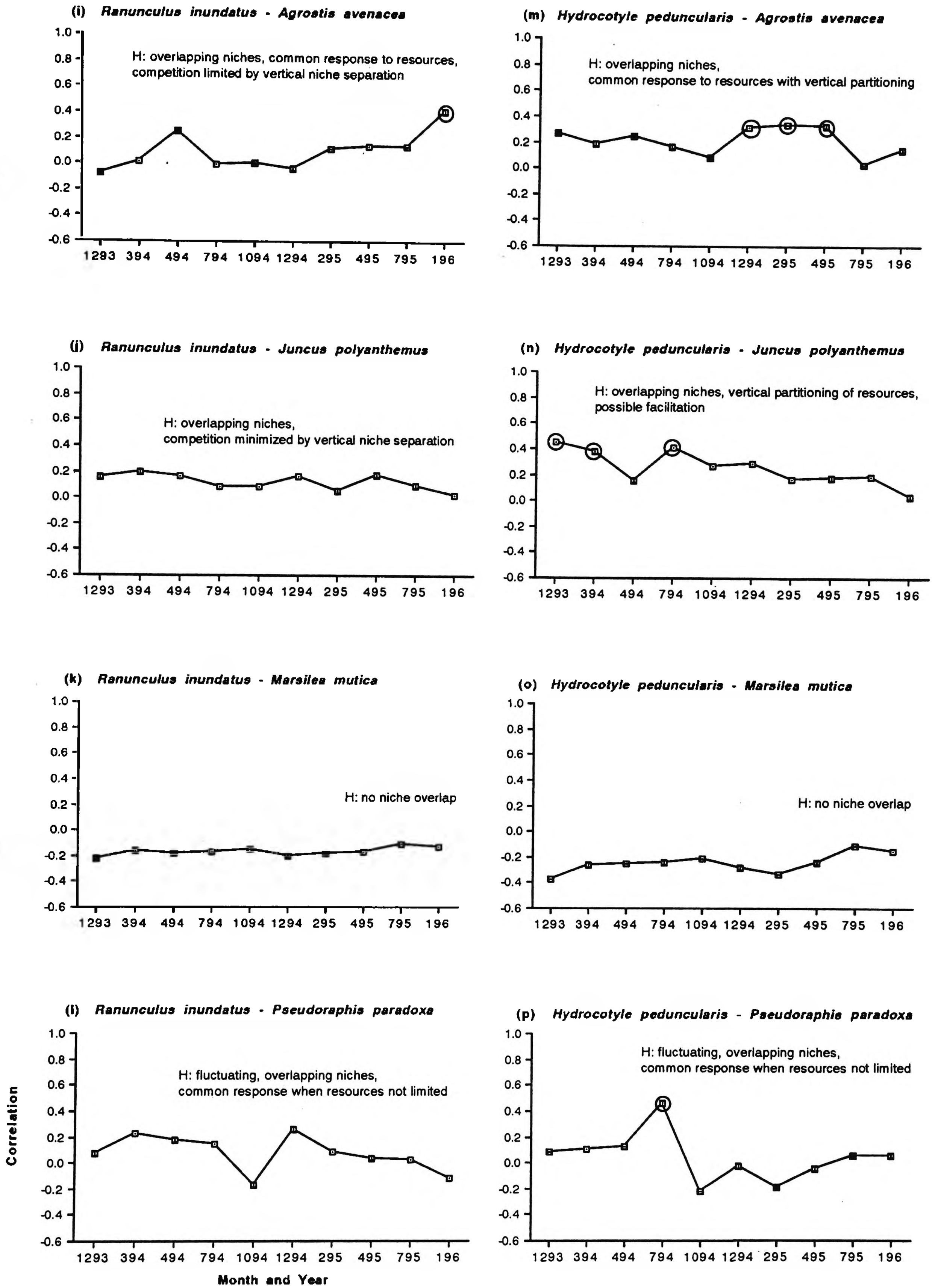


Figure 3.23 **(cont'd)** Changes in species pairwise covariances over two years along the wet meadow transition at Coomonderry Swamp.

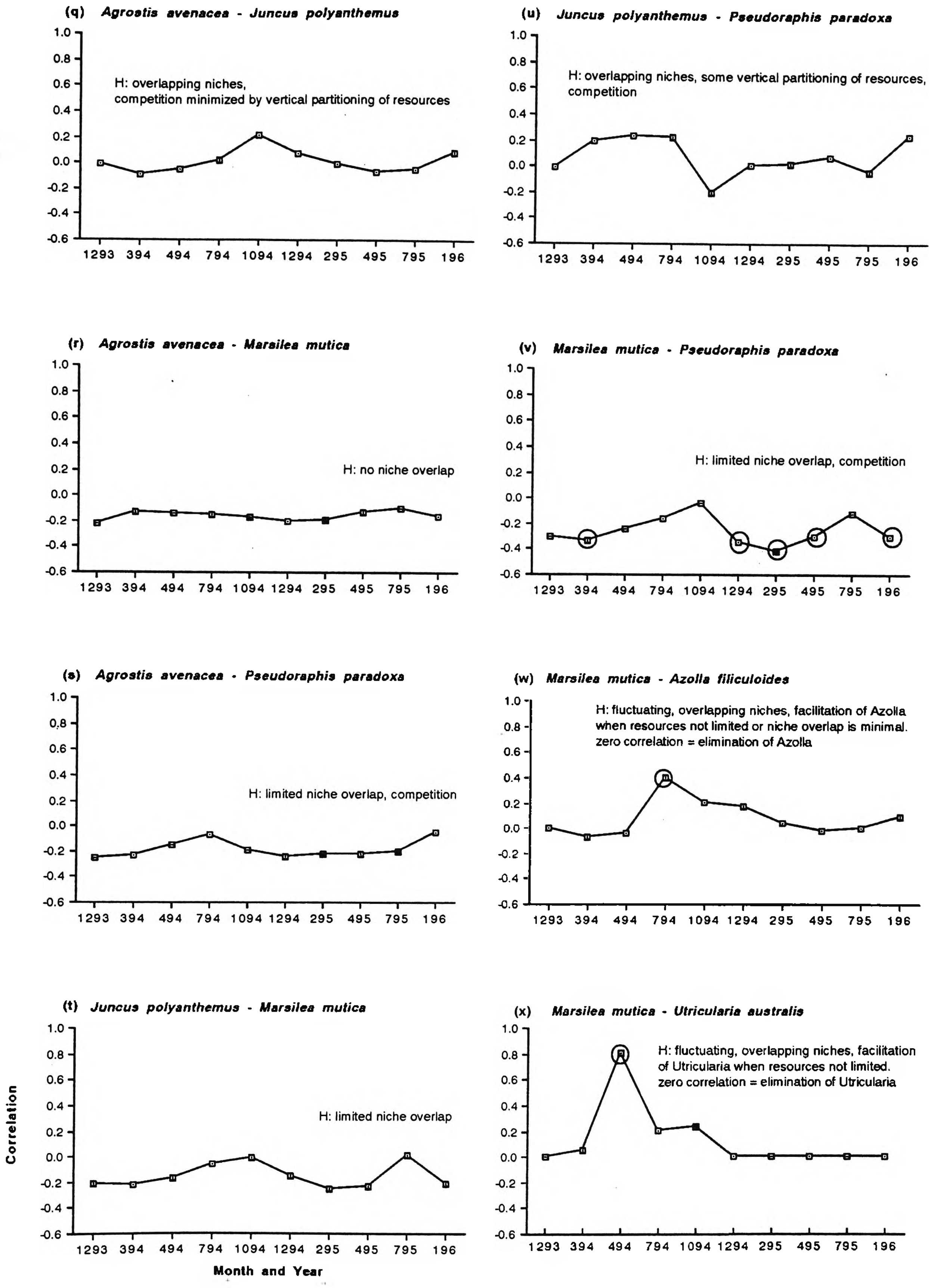


Figure 3.23 **(cont'd)** Changes in species pairwise covariances over two years along the wet meadow transition at Coomonderry Swamp.

Ludwig and Reynolds (1988) made some important points which emphasize the distinction between the association and covariance (correlation) between species pairs. These points need to be reiterated prior to discussion of the pairwise correlation results.

In the case of positive association, realized niche overlap (i.e. similar resource usage under existing conditions) is greater than expected by chance (Ludwig & Reynolds 1988). Plant species with overlapping distributions may be positively correlated because: (i) they have a common response to a supply of unlimited resources i.e. no interaction (the response of either species may be limited by other external biotic or abiotic factors such that competition is limited between the pair) or (ii) facilitation occurs (neighbours buffer one another from stressful conditions - Bertness & Shumway 1993). Alternatively, species with overlapping realized niches may be negatively correlated because of competition and species abundances fluctuate in unison in response to limited resources (Ludwig & Reynolds 1988).

Negative association suggests that: (i) species have different resource requirements, or (ii) competition results in exclusion. In both cases correlations will also be negative. Finally 'no association' or 'no correlation' could result from a balancing of opposing processes.

For each of the pairwise cases presented in Fig. 3.23, an hypothesis has been suggested (with varying degrees of confidence) regarding the cause for the observed temporal pattern of covariances. Some of these hypotheses are explained below. Of course the caveats of Section 3.4.2 apply. In particular hypotheses require experimental testing (c.f. Parrish & Bazzaz 1982; Wilson & Keddy 1986a & b; Zedler *et al.* 1990; Gaudet & Keddy 1995) not only because of the limitations suggested in Section 3.4.2, but also because examination of a single environment fails to reveal the extent of interactions (Colwell & Fuentes 1975).

Conditions along the upper part of the wet meadow transition were less subject to disturbance (in terms of inundation regime) and less stressful (in terms of disturbance and inundation effects) than the region at the lower end of the transition. Wet meadow had the characteristics of a late successional community (Parrish & Bazzaz 1982). It was dominated by perennial species which showed relative constancy in distribution and abundance through time (Ch. 3.3). Temporal vegetation dynamics were more extreme lower down the transition, ranging from a *Marsilea* dominated, 'deep water' community to an ephemeral, mud community. Both these communities were often characterized by early successional species (e.g. fast-spreading floating species and attached species in the former and annuals in the latter).

Thus the pairwise interactions measured undervalue the importance of pre-emptive competition in determining the composition and structure of wet meadow. However, some indication of the potential importance of the dominant species, *Isolepis prolifera* in dictating floristics through competition is illustrated by the negative correlations with secondary wet meadow species such as *Hydrocotyle peduncularis, Ranunculus inundatus* and *Agrostis avenacea.*

The zero to positive correlations between pairs of these secondary species (Fig. 3.23g,i, and m) were thought to indicate common responses to resources within the constraints applied by the presence of *Isolepis prolifera* and to a lesser extent *Pseudoraphis paradoxa.* I would expect that competition would be demonstrated in manipulated experiments between

Hydrocotyle peduncularis, Ranunculus inundatus and *Agrostis avenacea* in the absence of *Isolepis prolifera* and *Pseudoraphis paradoxa.*

Correlations in Fig. 3.23i,j,m,n,q and u are generally positive and I have suggested some amelioration of competition in wet meadow via vertical partitioning of resources related to life form (c.f. Grubb 1977). However it must be reiterated that there is some bias towards positive correlation because of the technique used (Fig. 3.23h).

Marsilea mutica was the only well distributed, consistently present component of the lower portion of the transition. Most correlations with *Marsilea mutica* were negative due to limited co-occurrences (Fig. 3.23e,i,k,o,r,t and v) but competition was hypothesised where there was niche overlap with *Isolepis prolifera* and *Pseudoraphis paradoxa.* Figure 3.23w and x support visual impressions of some facilitation of *Utricularia australis* and *Azolla filiculoides* and other species by *Marsilea mutica. Utricularia australis* and *Azolla filiculoides* were not usually present during drawdowns, or when *Marsilea mutica* formed a dense cover. Significant positive correlations coincided with autumn/winter high water levels when *Marsilea mutica* was less prolific (phenological restriction c.f. Yen & Myerscough 1989b). At these times, *Utricularia australis* and *Azolla filiculoides* (and other species) could occupy space within the *Marsilea mutica* mass, protected from wind and wave exposure. Not shown in Fig. 3.23w is the probable facilitation of *Azolla filiculoides* in January 1996 when it was prolific in a region of still water, protected by a band of outerlying *Marsilea mutica.* There may also have been facilitation (wind/wave protection) of *Marsilea mutica* by tall emergent species standing in deeper water. A shift down the elevation gradient by *Marsilea mutica* (Fig. 3.13) corresponded with the establishment of emergent species in previously open water. The consistent presence of *Azolla filiculoides* and *Spirodela* *punctata* in wind-protected waters below the *Melaleuca ericifolia* canopy in other parts of the wetland further suggests facilitation of these floating species (Figs. 2.10 & 3.21).

A range of investigations presented in this thesis (Chs. 2 & 3), as well as direct gradient analyses not presented, support the conclusions of Yen & Myerscough (1989a & b) concerning the coexistence of *Marsilea mutica, Ludwigia peploides* and *Myriophyllum* species. In wet meadow at Coomonderry Swamp, as at Bushell's Lagoon, Sydney, these species appear to be primarily differentiated in habitat niche, and where habitat niches overlap in water, they are differentiated along a gradient of exposure.

The most marked temporal fluctuations in correlations occurred between the two most dominant species of the wet meadow community - *Isolepis prolifera* and *Pseudoraphis paradoxa* (Fig. 3.23f). Correlations between these two species probably better approximate 'fundamental' responses (i.e. responses measured in the absence of all other species) than between any other species pairs. The species have a strong positive association (Fig. 3.20) (i.e. few double zeros) and diffuse interactions from other species would be minimized because few other species are found over much of their shared distribution (Fig. 3.13). I hypothesise that the coexistence of these two species is primarily maintained by differences in habitat and phenological niche and the fluctuations inherent in these (c.f. Grubb 1977; and 'transient niches' Comins and Noble 1985) (Table 3.3). I consider that these abiotic factors generally limit one or both species and consequently competition only sometimes (and in some places) becomes important. Significant positive correlations are considered to indicate a common response when both species have previously been restricted by abiotic factors. Similar arguments are considered to explain the fluctuations observed in covariances between other species pairs. Various studies, both practical and theoretical, have argued the importance of spatio-temporal environmental variability and species storage abilities in maintaining species coexistence and indefinitely delaying competitive exclusion (e.g. Bonis *et al.* 1995; Lavorel & Chesson 1995). The findings presented here, in Section 3.3 and Section 4.3 suggest that species richness in wet meadow at Coomonderry Swamp is maintained by these same processes.

In conclusion, most interactions beween species were relatively consistent through time. Competition was not well demonstrated by pairwise comparison of species in established wet meadow. However it was considered to be of greater importance here than at the lower, more stressful/high disturbance end of the transition. Evidence of pre-emptive competition is presented in Section 4.2, where it is shown that many species, whose seeds are present in the wet meadow seed bank, or whose seeds are dispersed into wet meadow, are generally prevented from germinating by the presence of existing species. The covariance data presented provide some limited support for the predictions of Bertness and Callaway (1994) i.e. facilitation appeared to be an important determinant of the presence of some aquatic species.

3.5 Ecological Profiles

There remains a great need for widely available, published information on the ecology of NSW wetland plants, although some texts deal well with the biology and provide some general ecological characteristics of species (Sainty & Jacobs 1981, 1988; Harden 1990-93). Books providing detailed information on habitat, propagation and establishment have been published for other regions and have some value to wetland managers in NSW. For example, the comprehensive account of the ecology of common British plant species by Grime *et al.* (1988) lists some species and genera found in NSW.

Chambers *et al.* (1995) have produced an excellent field book on the biology and ecology of 14 wetland species, many of which are common to NSW. Their work represents an important beginning, but many more species require attention and, as Chambers *et al.* (1995) caution, their information was based on only one wetland over two annual cycles.

Similarly, in this research, much valuable ecological data was accumulated on many wet meadow and deeper water herbaceous, wetland plants. Brief ecological profiles of some of these species are given in Table 3.5. Table 3.5 also provides notes on depth ranges of species from where they occur at wetlands on the south coast of NSW and from information provided in other studies. Further research will be needed on propagation techniques and establishment requirements (c.f. Casanova and Brock 1996), although in Section 4.3, seasonal variation in establishment of some herbaceous species is examined.

Adam *et al.* (1985) noted that in some cases wetland boundaries, delineated by aerial photography, are not distinct. They noted, in particular, the transition from wetland (often wet meadow) to agricultural land. A benefit, originally conceived for compiling ecological profiles of wet meadow species at Coomonderry Swamp, was to identify potential indicators of boundaries. It was hoped that species, or suites of species might be identified which had narrow distributions at the upper wetland margin, but which were also common to most unwooded (degraded), freshwater wetlands. Such species would also need to be relatively persistent and seasonally constant. Inspection of Table 3.5 and the findings of Ch. 2 did not suggest species, or even groups of species ideally suited for the purpose. Species listed in Table 3.5 as having narrow (dry) elevation ranges may have some function in this regard, although it is expected that some, or all, will have varying distributions when more or less constrained by biotic interactions under

Table 3.5 Ecological profiles of some species of the wet meadow transition at Coomonderry Swamp.

Species	Seasonal senescence	Response to inundation	Elevation range	Inundation regime	Notes	Suitablity as an indicator
Persicaria decipiens Decumbent to ascending herb. Annual or perennial.	+++	++++	broad (dry - wet)	odr: -23±5 to -21±5 adr: -70 to 55 fluctuations: 1.3	Similar optimum depth range at Killalea and Brundee wetlands.	Low
Persicaria hydropiper Erect or ascending herb. Annual or perennial.	++++	++++	narrow (dry)	odr: -23±5 to -22±6 adr: -70 to 52 fluctuations: 1.3		Low
Persicaria praetermissa Prostrate to decumbent herb. Perennial.	++++	+++	narrow (dry)	odr: -24±5 to -23±5 adr: -70 to 45 fluctuations: 1.3	Similar optimum depth range at Brundee Swamp.	Low
Bidens tripartita Introduced annual.	+++++	++++	narrow (dry)	odr: -25±5 to -23±6 adr: -70 to 52 fluctuations: 1.3		Low
Agrostis avenacea Tufted rhizomatous, annual or perennial.	++++	+	narrow (dry)	odr: -22±6 to -20±5 adr: -70 to 19 fluctuations: 1.3	Tolerates brackish conditions at Brundee. Similar depth range at Killalea and Brundee.	Moderate
Hydrocotyle peduncularis Prostrate to ascending, stoloniferous herb. Perennial.	++++	+	narrow (dry)	odr: -22±6 to -17±5 adr: -70 to 19 fluctuations: 1.3		Low

...cont'd

Species	Seasonal senescence	Response to inundation	Elevation range
Juncus polyanthemus (+ hybrids) Shortly to strongly rhizomatous perennial.	+	+	broad (dry - mid)
Ranunculus inundatus Rhizomatous or stoloniferous, perennial herb.	++	+	narrow (dry)
Juncus procerus (+ hybrids) Strongly rhizomatous perennial.	+	0	narrow (mid)
Eleocharis acuta Rhizomatous perennial	+++	0	broad (dry - wet)
Pseudoraphis paradoxa Stoloniferous perennial.	+++	+	broad (upper - mid)

...cont'd

Inundation regime	Notes	Suitablity as an indicator
odr: -25±5 to -17±5 adr: -70 to 57 fluctuations: 1.3	Similar depth ranges at other sites, including estuarine upper margins but difficult to identify.	Moderate
odr: -20±5 to -14±5 adr: -70 to 19 fluctuations: 1.7	Response to inundation much greater at other sites e.g. Sainty & Jacobs (1981); 30cm water at Killalea. Suggests competitive exclusion.	Low
odr: -25±6 to -24±5 adr: -70 to 42 fluctuations: 1.7	Not widespread.	Low
odr: -11±6 adr: -70 to 32 fluctuations: 4.0	Sporadic at Coomonderry Swamp. Similar range at Killalea, Brundee and Terrara. Described as tolerating wide seasonal fluctuation by Chambers *et al.* (1996) (i.e. -0.2 to 0.4). Similar range at Killalea, Brundee and Terrara.	Low
odr: -24±5 to 7±5 adr: -70 to 48 fluctuations: 3.0	Similar depth range at other Coomonderry sites and Sainty & Jacobs (1981).	Low

Species	Seasonal senescence	Response to inundation	Elevation range	Inundation regime	Notes	Suitablity as an indicator
Isolepis prolifera Stoloniferous perennial. Introduced.	++	++	broad (dry - mid)	odr: -11±5 to 24±5 adr: -70 to 57 fluctuations: 3.0	At Coomonderry Swamp competitively excludes other species over optimum depth range. Seasonal fluctuation: -0.2 to 0.2 (Chambers *et al.* 1996). Similar range at Killalea.	Low
Paspalum distichum Rhizomatous and stoloniferous perennial.	+++	+++	narrow (mid)	odr: 6±5 to 14±5 adr: -70 to 47 fluctuations: 2.3	Similar depth range given by Sainty & Jacobs (1981).	Moderate
Marsilea mutica Rhizomatous perennial.	+++	++++	narrow (wet)	odr: 6±5 to 39±5 adr: -54 to 85 fluctuations: 2.7	Similar depth range at Brundee Swamp and given by Sainty & Jacobs (1981) and Yen & Myerscough (1989a).	Moderate
Ludwigia peploides Erect or stoloniferous. Creeping or floating.	+++	++++	broad (dry - wet)	odr: 9±5 to 39±5 adr: -70to 85 fluctuations: 2.7	Mostly sporadic but widely distributed. Similar depth range at Killalea wetland and given by Sainty & Jacobs (1981) and Yen & Myerscough (1989a).	Low

Odr: optimum depth range (cm) calculated from inundation data following inspection of direct gradient analyses (n = 16) over three years. Adr: absolute depth range for each species over three years (species may not have survived long at these extremes). Negative values are estimated water table depths and positive values are above ground water depths. Upper values of odr and adr were limited by the transect length. Elevation range refers to the region over which the plant tolerated inundation conditions i.e. often greater than odr, but less than adr. Fluctuations: mean number of wet to dry alternations per annum (3 years of record). Seasonal senescence and response to inundation are graded high (+++++) to undetected (0). Criteria for classification as suitable indicator species is discussed in the text.

different abiotic conditions. Clearly, the usefulness of herbaceous wetland plants as indicators of boundaries requires the collation of more data.

Much more clearly defined over broad geographic areas were the wetland boundaries of wooded margins and of upper saltmarsh (Section 2.3) and these can usually be determined from aerial photography (Adam *et al.* 1985). However, for sites threatened by development, there will still be disagreement about actual water's edges and buffer zones, even where margins appear well delineated by aerial photography. I consider that boundaries (and the start of appropriately sized buffer zones) at such sites will still need to be defined in the field (on a site by site basis) by the identification of regions dominated by wetland species. For example, for wet meadow those species listed in Tables 3.3 & 3.4 (as opposed to pasture species) and at estuarine sites, species such as *Juncus kraussii* and *Baumea juncea*.

3.6 Summary

3.6.1 Spatial dynamics at Coomonderry Swamp

(i) Zonations (community divisions) along both the wet meadow transition and the open-forest - wetland transition were found to be spatially consistent and temporally stable.

(ii) In herbaceous vegetation the major transition was a distinct shift from species rich wet meadow to a *Marsilea mutica* dominated deepwater community, or at other times, to an ephemeral mud community. This shift occurred below the modal water's edge.

(iii) In woody vegetation, the boundary between *Eucalyptus botryoides* open-forest and the *Eucalyptus robusta - Gahnia sieberiana* community was diffused along a soil organic matter gradient. The boundary separating the latter community from *Melaleuca* scrub (Site 2) and from sedgeland (Site 3) was abrupt and occurred at the water's edge.

3.6.2 Long term vegetation change at Coomonderry Swamp

(i) Aerial photography allowed recognition of major vegetation boundaries only.

(ii) There has been little change in the size and shape of Coomonderry Swamp over the past 50 years.

(iii) Over that time, there has been a decrease in open water areas, a possible decrease in *Melaleuca* scrub, and an increase in *Typhus orientalis*. Drainage channels were visible in the 1949 aerial photo.

(iv) The most important change along the swamp - forest dunal transition has been the construction of the road through the open-forest in the early 1970's.

3.6.3 Short term vegetation dynamics along the wet meadow transition at Coomonderry Swamp

3.6.3.1 Whole transition dynamics

(i) Herbaceous vegetation along the southern margin of Coomonderry Swamp was subject to an inundation regime which responded rapidly to rainfall and dry weather. There were marked variations in the size and duration of wet - dry cycles over the 3.5 years of survey. The number of wet - dry fluctuations, and the depth and duration of flooding also varied greatly along the elevation gradient.

(ii) Whole transect dynamics were not well indicated by cluster and ordination techniques. Short term vegetation dynamics were masked by the constancy of dominant species and the inertia of the system (vegetation change lagged behind change in physical conditions). However, changes in vegetation wrought by variation in season or inundation were visually pronounced, and were qualitatively analyzed, using a sequential photographic record.

3.6.3.2 Community dynamics

(i) The wet meadow community (upper 150 m of the transition) remained constant and resilient despite inundation and seasonal flux.

(ii) Community dynamics were much greater at lower elevations (lower 100 m of the transition). A *Marsilea mutica,* deepwater community predominated but, during dry periods, drawdowns allowed establishment of ephemeral mud communities. When reflooded, these developed into emergent stands at the lowest part of the transition.

(iii) Community dynamics were most strongly correlated with the 'inundation index', which was based on a three year record of the number of wet - dry cycles and the cumulative length of time intervals along the elevation gradient were inundated (Table 3.2).

(iv) Species richness was also significantly correlated with the inundation index, being much greater in wet meadow and ephemeral communiites than in deepwater communities.

3.6.3.3 Species dynamics

(i) Species are limited in distribution by a range of factors, but numerous experiments have shown that in wetlands inundation regime is the primary determinant. Temporal surveys under field conditions do not commonly show limiting effects, but more often show responses (often subtle) within an existing range.

(ii) The major dominant species showed little change in their distributions over time.

(iii) While species dynamics were often subtle, they were confirmed by the disparate techniques of direct gradient analysis, cluster analysis and ordination.

(iv) Species varied in their response to season. *Bidens tripartita, Pseudoraphis pararadoxa, Marsilea mutica* and *Paspalum distichum* were important species showing marked winter reduction in abundance. *Isolepis prolifera* showed some winter senescence, while *Juncus* spp. showed little winter reduction.

(v) Species showed some variation in their response to inundation. For example: *Paspalum distichum* was most abundant over its distribution in dryer conditions; *Marsilea mutica* showed a temporal shift into deeper water hypothesised to reflect the wind and wave buffering effects of emergent vegetation in deeper water. *Bidens tripartita* was prevalent during dry periods when more gaps were available.

(vi) Season and inundation effects were not independent. For example *Isolepis prolifera* showed greatest abundance at the upper elevation during wet summers following dry winters. At lower elevations very dry summers resulted in an ephemeral community while *Marsilea* dominated in wet summers.

3.6.4 Short term vegetation change along the open-forest - *Melaleuca* transition at Coomonderry Swamp

(i) There was little change in woody or herbaceous vegetation along the Open-forest - Melaleuca transition over three years.

(ii) There was much less change in the species composition and abundance in standing water below the *Melaleuca* canopy than in deep, open water of the wet meadow transition.

3.6.5 Species interactions along the wet meadow transition at Coomonderry Swamp

(i) Most pairwise correlations between species of the wet meadow transition were negative, suggesting either niche separation, competitive exclusion or competitive fluctuation (where species overlap was substantial).

(ii) Competition generally, was hypothesised to be of increasing importance in determining vegetation structure towards the drier, more mesic end of the wet meadow transition. In particular, pre-emptive competition was thought to limit the opportunities for establishment of transient species.

(iii) At lower elevations, there may have been evidence of facilitation following disturbance. For example *Azolla filiculoides* flourished in water protected from wind and waves by *Marsilea mutica.*

(iv) At lower elevations both drawdown and flooding resulted in large gaps available for opportunistic species. Interspecific competition would rarely have been significant, perhaps only when *Marsilea mutica* densely covered open water during wet summers, or when ephemeral communities had sufficient time to develop during prolonged drawdown.

(v) There was some evidence that positive correlations between some species pairs were the consequence of a common response to resources. In some cases, competition was thought to have been ameliorated by vertical partitioning.

(vi) There is some support for the hypothesis of Bertness and Calloway (1994) that competition is more important in benign habitats and facilitation has a greater role in harsh environments. However facilitation resulting from vertical vegetation structure requires study.

(vii) Most pairwise species interactions remained consistent through time.

(viii) Significant temporal fluctuations in correlations occurred between some species pairs, and in particular, between the two primary species of wet meadow: *Isolepis prolifera* and *Pseudoraphis paradoxa.* It is considered that the coexistence of these two species is maintained by differences in habitat and phenological niche and the fluctuations in these. I suggest that positive correlations indicated common responses when both species were previously limited and that competition resulted when one or both species were favoured by prevailing conditions.

3.6.6 A cyclic model of dynamics along the wet meadow transition at Coomonderry Swamp

(i) No directional (successional) changes in vegetation were identified in this short term study. However natural regeneration of woody species within the wet meadow is being photographically monitored and is reported in Chapter 4.

(ii) A process of cyclic change was observed at lower elevations along the wet meadow transition. The following community changes were observed: open water with few species; deep water dominated by floating species (e.g. *Marsilea mutica*); deep water dominated by tall emergents; and ephemeral mud communities. Wet meadow is hypothesised to represent a later successional stage of the ephemeral community which has developed under a more benign regime of inundation at higher elevations.

(iii) The pattern of cyclic change in herbaceous vegetation observed at Coomonderry Swamp was also noted at Killalea wetland (Ch. 2). It corresponds well to the generalized model of van der Valk (1981).

3.6.7 Ecological profiles

(i) Spatial and temporal data on the ecology of species can be used to construct ecological profiles. Ecological profiles, with biological and propagation information, are needed for conservation and restoration purposes.

(ii) Caution needs to be applied in the present case (Table 3.5), where profiles were largely compiled from species abiotic and biotic responses at one wetland over three years. Research over a greater range of field conditions is needed with support from well designed manipulated experiments (c.f. Grime *et al.* 1988).

3.7 Conclusion

At the southern end of Coomonderry Swamp, the wet meadow community of upper elevations remained relatively constant in species composition. Minor variations in the distribution and abundance of dominant species were considered to reflect fluctuations in competitive abilities primarily in response to seasonal and inundation change (both spatial and temporal). This spatial and temporal variation offered transient opportunities for secondary perennial species and annuals.

Lower on the elevation gradient, more extreme conditions resulted in an alternation of communities. Communities rarely progressed beyond an early successional stage, thus competiton was thought to be less important in determining structure.

While extensive clearing of land abutting the margin at Coomonderry Swamp had occurred early this century, the photographic record of the last fifty years indicated little further change despite drainage. Long term monitoring will be needed to identify any successional processes which may result from a recent increase in residential and agricultural pressures on the catchment.

Melaleuca ericifolia

Chapter 4 Ecological implications of a woody plant restoration experiment.

4.1 Introduction

Freshwater wetlands are not common on the south coast of NSW, Australia. Fewer still retain stands of 'natural' woodland margin. Most remaining wetlands have been converted by clearing and grazing into small rush and sedge swamps fringed by wet meadow.

The few studies which have investigated establishment requirements of emergent aquatic macrophytes have concentrated on their introduction into newly created sites, either for the purposes of wastewater treatment or for the revegetation of previously mined areas. In the latter case, the choice of non-woody species might result in vegetation structure similar to that found in degraded freshwater wetlands on the NSW south coast.

Recognition of the intrinsic worth of wetlands has been accompanied by numerous attempts at restoration and some examples of wetland creation *de novo*. As indicated in Section 1.7, most of these are coordinated by local authorities or conservation groups on a site-by-site basis. Most involve at least some planting of indigenous woody species, yet there is little widely communicated information available on the ecology of these species or on efficient methods for their establishment (c.f. Zedler 1996 for saltmarsh restoration). In fact, the literature on the use of woody plants in wetland restoration generally is very sparse (Mitch & Gosselink 1993; Adam 1995). In addition, management policies are now prescribing restoration or compensation where wetlands are degraded or lost, despite the absence of adequate information on propagation and planting (e.g. Illawarra Catchment Management Committee 1993; Department of Land & Water Conservation 1996).

In Section 1.3, I argued that Coomonderry Swamp was potentially an important reference site for freshwater wetland restoration on the south coast of NSW. Surveys at other local wetlands, and comparisons to other regions in NSW, presented in Chapter 2, confirmed that this was the case. Firstly, undisturbed wetland margins on the south coast of NSW differ from their northern counterparts. For example, *Melaleuca quinquenervia,* a dominant of many northern wetlands, does not occur naturally south of Sydney, where it is commonly replaced by *Melaleuca ericifolia*. Secondly, as indicated earlier, freshwater wetlands with an extensive, undisturbed wooded component are rare in south coastal NSW.

The work presented in Chapter 2 revealed that only a few woody species dominate the margins of both freshwater and estuarine wetlands in the region. Almost all of these are found at Coomonderry Swamp. The experiment described in this section was carried out at Coomonderry Swamp within wet meadow which had been previously cleared and grazed. Given the premise that wet meadow is an intermediate goal of many fabrication projects and a starting point for enhancement of degraded sites on the NSW south coast (Fig. 4.1), the objective was to provide initial information on establishment success of key indigenous woody species within existing wet meadow under varying planting regimes.

During the experiment, temporal monitoring of plots and the surrounding vegetation provided the opportunity to collect further data on spatial variation within wet meadow and inundation and seasonal effects on weed versus indigenous plant invasion. These data, also analysed in this chapter, proved to be an invaluable adjunct to other work undertaken on vegetation dynamics at Coomonderry Swamp (Ch. 3).

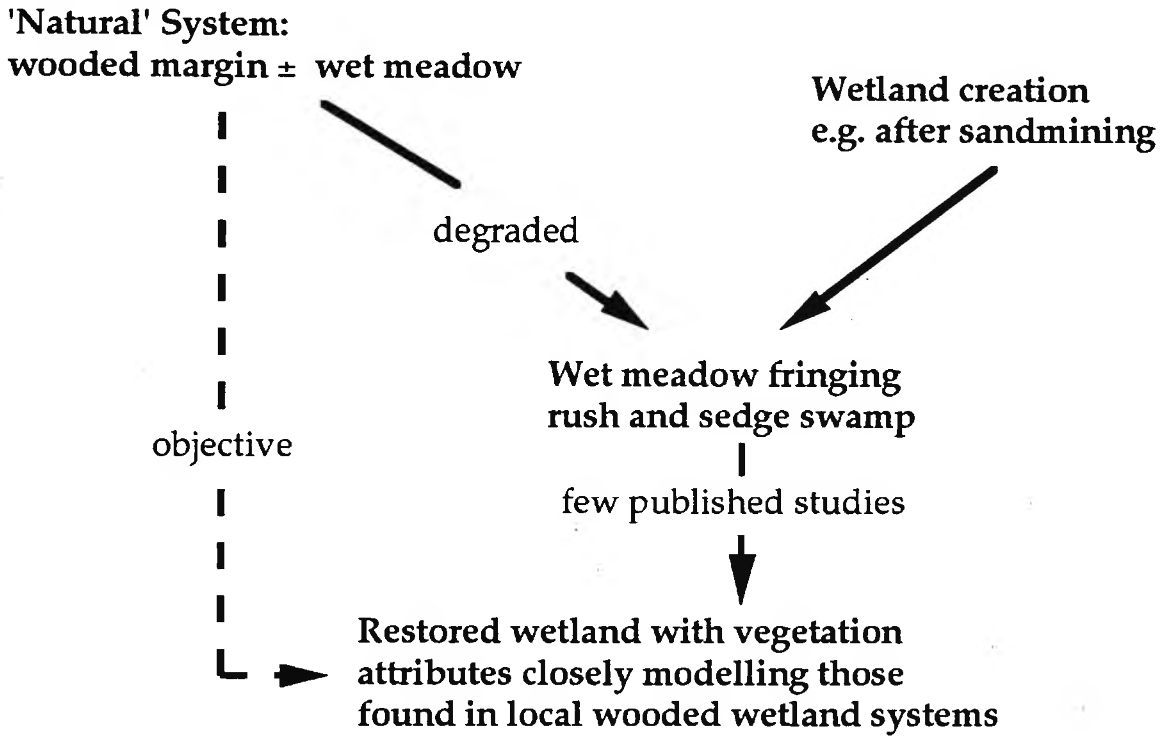


Fig. 4.1 Wetland dominated by herbaceous species is the starting point of many restoration projects on the south coast of NSW, Australia.

4.2. Establishment of indigenous woody species within coastal, freshwater wet meadow

4.2.1 Aim

To investigate the relative establishment success of seeds and tubestock from five indigenous woody species following planting in previously cleared and grazed wet meadow.

4.2.2 Methods

Seeds of *Eucalyptus robusta, Casuarina glauca, Leptospermum juniperinum, Melaleuca ericifolia* and *Melaleuca linariifolia* were collected from trees (several of each species) on the margins of Coomonderry Swamp in March 1994 (an illustration of the flowers and fruits of each species has been used as a frontispiece to the chapters of the thesis). Seedlings were raised in seed trays containing a perlite, vermiculite, peat moss, seed-raising mix, under glasshouse conditions (May 1994, ≈ 100% germination). Seedlings were individually potted into 5 cm diameter tubes (10 cm depth) containing a commercially prepared soil for natives (late June - September 1994, ≈ 100% survival). Seedlings of a sixth species, *Callistemon citrinus,* were successfully propagated but due to time constraints were not planted.

Seeds (≈ 50 per plot) and tubestock were planted at two elevations (Fig. 4.2) in previously cleared and grazed wet meadow adjacent to Transect 1. Logistical constraints required that planting was staggered: (i) tubestock - 24th December 1994 to 18th February 1995; (ii) seeds - 11th March 1995 to 3rd May 1995). However, planting (of either seeds or tubestock) at both elevations for each species was carried out at the one time and no statistical comparison was subsequently carried out among species, or between seeds and tubestock. Subsamples were planted in a randomized design with three

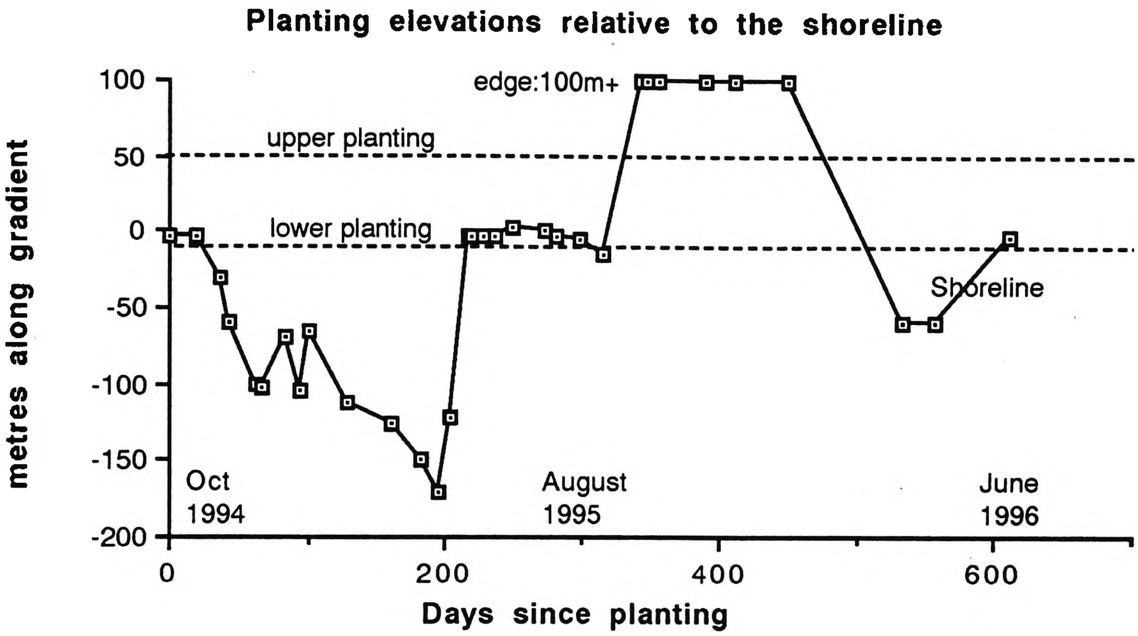


Fig. 4.2 Fluctuations in inundation experienced at the two planting elevations during the experiment.

plot treatments: 'W' cleared and weeded every two months; 'C' cleared and left; 'U' uncleared. Tubestock and seeds were planted at approximately 1 m intervals in 15 rows of 20 plants at each elevation (Fig. 4.3). Plots were approximately square with 25 cm sides for the cleared and weeded, and cleared and left treatments. For the unweeded treatment, a notch was placed in the ground without removal of existing vegetation and the soil was pressed around each seedling as it was planted into the notch. Total plots for each species were 600 i.e. randomized allocation of: stock (tubed seedling or seeds) (2) x treatments (3) x elevations (2) x replicates (50). In a few cases plots were wrongly marked or saplings died or were destroyed by cattle. This small variation in the number of plots is shown in result tables and figures.

Survivorship and growth were monitored over nine months, after which time differences between seeds and tubestock and among species were already apparent. To comply with local Council requests and to reduce labour, most tubestock were removed at that stage. However ten saplings of each species at each elevation were randomly chosen and retained for longer term monitoring. Growth and survivorship of these plants after 20 months are presented.

Records were maintained on variations in inundation over the 20 months at each planting elevation (Fig. 4.2). During a drawdown in May 1996, soil profiles were examined, and soil samples collected, at each planting elevation along the adjacent Transect 1. The following tests were performed by the Soil and Water Testing Laboratory, Scone Research Service Centre, NSW (Department of Land and Water Conservation): texture, acid sulfate potential (one sample, upper elevation), Emerson aggregate test, total kjeldahl nitrogen, total phosphorus, pH, total cation exchange capacity and exchangeable Na, K, Ca, Mg and Al cations and available water capacity (field

Figure 4.3 The planting matrix for *Eucalyptus robusta.*

capacity and wilting point). To meet the needs of Chapters 2 and 3, pH and electrical conductivity were measured at other intervals along Transect 1, and the whole suite of tests was performed on a soil sample 200 m along Transect 1. At the time of planting, vegetation type and height surrounding each plot were noted. Records were also kept every two months on neighbouring species which vegetatively spread into weeded plots, and of species established in plots from seed.

During this project, the progress of natural woody plant regeneration was photographically monitored within the wet meadow area.

4.2.3 Results

4.2.3.1 *Soils*

There were only minor differences in soil characteristics between the samples at the two planting elevations and a third sample from even lower on the elevation gradient (Table 4.1). Soil profiles (Fig. 4.4) showed a consistent structure along the wet meadow transition: a dense plant root zone (5-20 cm) with increasing dead plant material at lower elevations; a 'sticky' dark brown horizon (to approximately 30 cm); a harder more friable, more impervious darker horizon. Transitions to the water table were distinct.

Surface soils along the transition were highly organic, making texture difficult to assess. Soils were moderately acidic, but with no related metal toxicity. Salinity was uniformly low. Cation exchange capacity was moderate, with most cations available except potassium and aluminium. Sodicity was very high, but progressively lower at lower elevations. Surface soils had high waterholding capacity, available phosphorous was probably low and available nitrogen was probably high. Acid sulfate potential was high.

Table 4.1 Soil characteristics along the wet meadow transition at Coomonderry Swamp.

Characterisitic	**Upper elevation** 40 m along transect	**Lower elevation** 120 m along transect	200 m along transect
Texture	loam	loam	loam
Emerson aggregate test	5	8/3 (1)	8/3 (1)
Total Nitrogen (%)	1.22	0.89	0.75
pH	4.6	5.2	5.2
Elect. Cond. (dS/m)	0.33	0.19	0.15
Phosphorus (mg/kg)	3	1	1
AWC: FC (%)	104.4	78.2	81.8
WP (%)	38.9	28.9	27.5
CEC & exch. C (me/100g):	21.2	19.6	21.3
Na	5.5	3.1	2.9
K	0.2	0.2	0.4
Ca	7.3	7.2	8.0
Mg	3.3	4.0	5.4
Al	nd	nd	nd

Due to cost constraints, data are for single samples only. Soils were collected at 15 - 25 cm depth (Fig. 4.4). AWC - available water capacity; FC - field capacity; WP - wilting point; CEC - cation exchange capacity; exch. C - exchangeable cations; nd = not determined. Upper and lower refer to planting elevations.

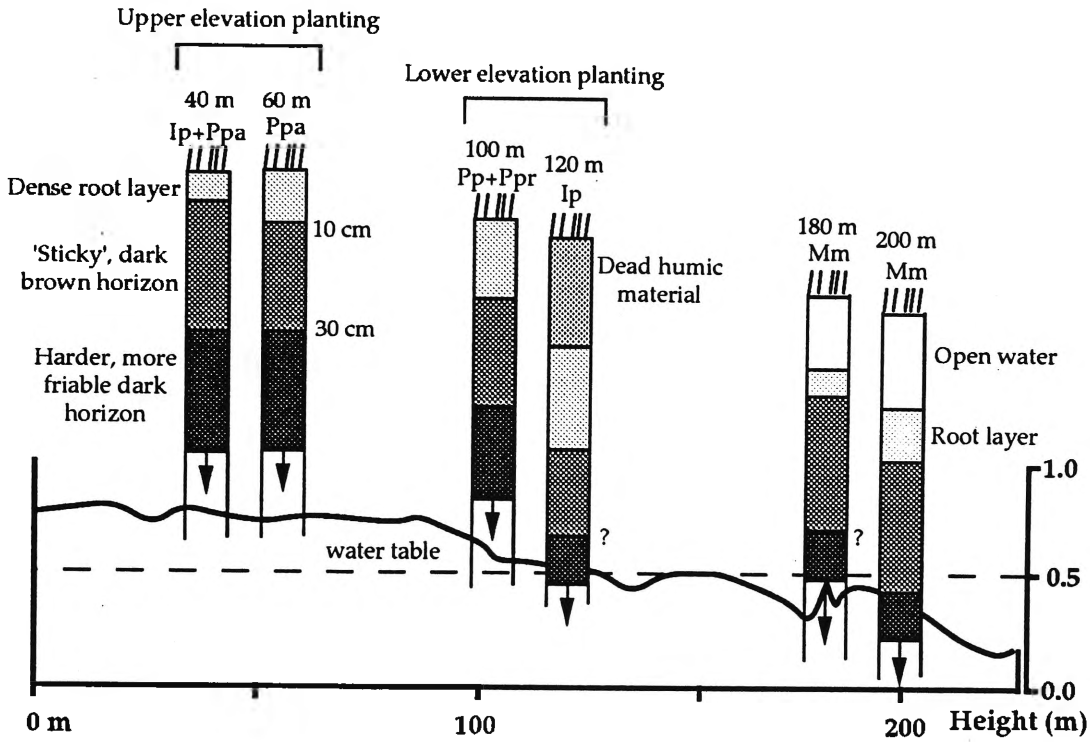


Figure 4.4 Soil profiles along the wet meadow transition at Coomonderry Swamp.

4.2.3.2 *Seeds*

Few seeds of any species germinated in uncleared plots (Fig. 4.5). Proportions of cleared plots with seedlings after two months ranged from 24% to 57% at the upper elevation, but were significantly higher for all species except *Melaleuca linariifolia* at the lower elevation (40% to 94%) (Appendix 10). Upper plots were much dryer over this time (Figs. 4.2 & 4.5).

Figure 4.6 indicates the differences in inundation, surrounding vegetation and encroaching species between initially cleared plots at upper and lower planting elevations. Few seeds in each plot germinated even at the lower, wetter elevation (Table 4.2). The proportions of seeds germinating in each plot at the upper elevation and the moisture/exposure characteristics of the plot were significantly positively correlated for all species except *Casuarina glauca* (Table 4.3). Vegetation surrounding plots and germination success were not correlated except for the lower elevation planting of *Melaleuca linariifolia*. Vegetation height was significantly higher here than elsewhere (Table 4.3). Survivorship of seedlings decreased rapidly (Fig. 4.5) following a period of prolonged saturation at the upper elevation and inundation at the lower elevation. Inundated plots invariably became densely matted with algae and a red precipitate (probably iron oxy-hydroxide) was often evident.

4.2.3.3 *Plants*

Almost all tube stock, irrespective of species or planting treatment, survived the first nine months of dryer conditions (Fig. 4.7). However, there were interesting differences in stem diameters and plant heights among treatments and between the two planting elevations (Figs. 4.8 & 4.9). In general, species showed better growth at lower elevations, particularly in uncleared plots. In contrast, at upper elevations, growth for most species was

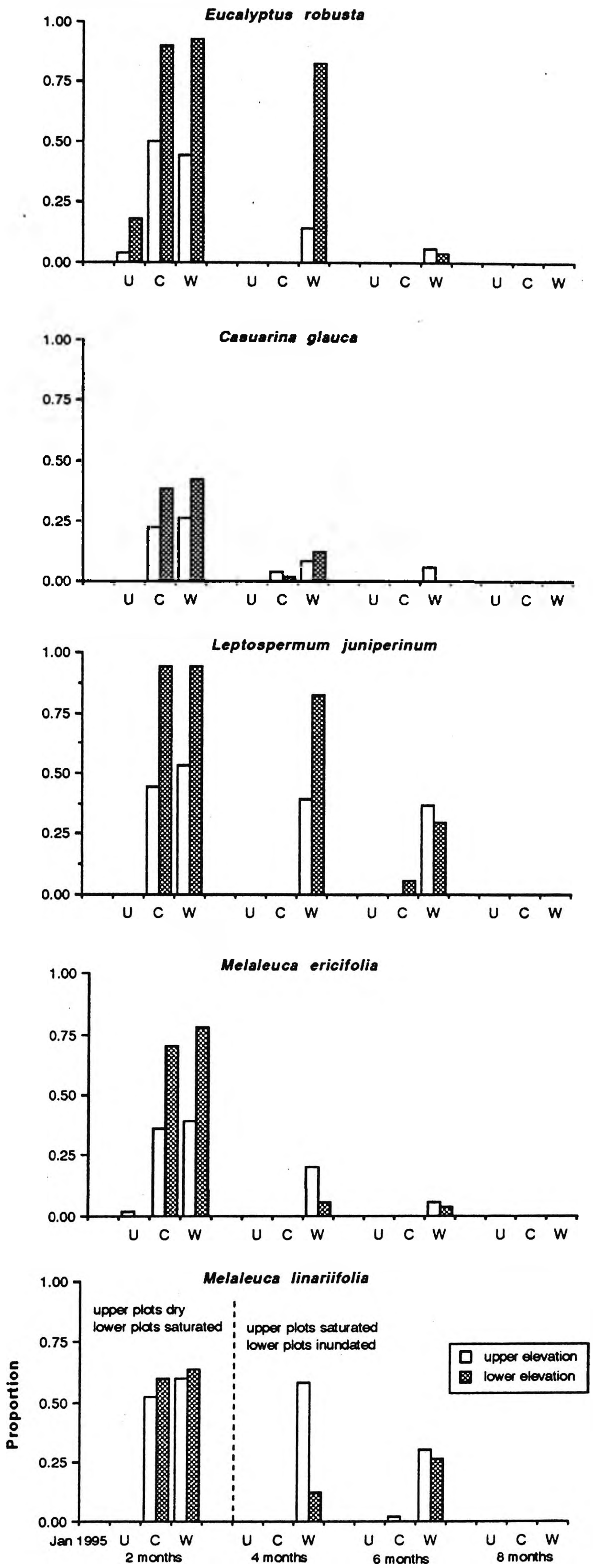


Figure 4.5 Proportions of plots with seedlings at intervals over eight months at upper and lower planting elevations in wet meadow. 'U' - uncleared plots; 'C' - cleared plots; 'W' - cleared & weeded plots. 'n' plots 50 ± 2.

A

B

Figure 4.6 Seedlings of: **A** - *Leptospermum juniperinum* (upper elevation plot); and **B** - *Eucalyptus robusta* (lower elevation plot).

Table 4.2 Mean proportion of seeds of five woody species germinated after two months in each plot at two elevations in wet meadow.

Species	Elevation	Cleared Mean (SE)	Uncleared Mean (SE)
Eucalyptus robusta	upper	0.01 (0.00)	0
	lower	0.11 (0.01)*	0.01 (0.01)
Casuarina glauca	upper	0.02 (0.01)	0
	lower	0.02 (0.01)	0
Leptospermum juniperinum	upper	0.04 (0.01)	0
	lower	0.18 (0.02)*	0
Melaleuca ericifolia	upper	0.02 (0.01)	0
	lower	0.12 (0.02)*	0
Melaleuca linariifolia	upper	0.06 (0.01)	0
	lower	0.12 (0.02)*	0

Proportions calculated on an estimated 50 seeds placed in each plot. Mean prop. greater at lower elevation than at upper elevation are indicated (* $P < 0.05$ - Tukey test following ANOVA). 'n' plots: 50 ± 2.

Table 4.3 Plot characteristics and their correlations with proportions of seeds of five woody species germinated in initially cleared plots after two months.

Species	Elevation	Exposure index mean	Exposure index r	Surrounding vegetation height mean	Surrounding vegetation height r
Eucalyptus	upper	1.9 (0.1)	0.32**	29 (1)	0.09
robusta	lower	3.4 (0.1)***	0.15	39 (3)*	0.12
Casuarina	upper	2.2 (0.1)	0.19	37 (3)	0.08
glauca	lower	4.0 (0)***	-	44 (3)	-0.05
Leptospermum	upper	2.7 (0.1)	0.33**	44 (3)	0.15
juniperinum	lower	3.8 (0.1)*	0.23*	58 (5)	0.09
Melaleuca	upper	1.9 (0.1)	0.53***	37 (3)	0.09
ericifolia	lower	3.0 (0.1)***	0.21*	39 (1)	0.05
Melaleuca	upper	2.2 (0.1)	0.36***	27 (2)	0.87
linariifolia	lower	3.5 (0.1)***	-0.06	75 (5)***	0.21*

Exposure index - plots were ranked as: 1 - dry and open, 2 - dry and overgrown by invading weeds, 3 - moist and overgrown by invading weeds, 4 moist and open. Surrounding vegetation height measured in centimetres. Standard errors in parentheses. 'n' plots: 100 ± 2. *Significant at $P < 0.05$; **significant at $P < 0.01$; ***significant at $P < 0.001$ (T test - two tailed).

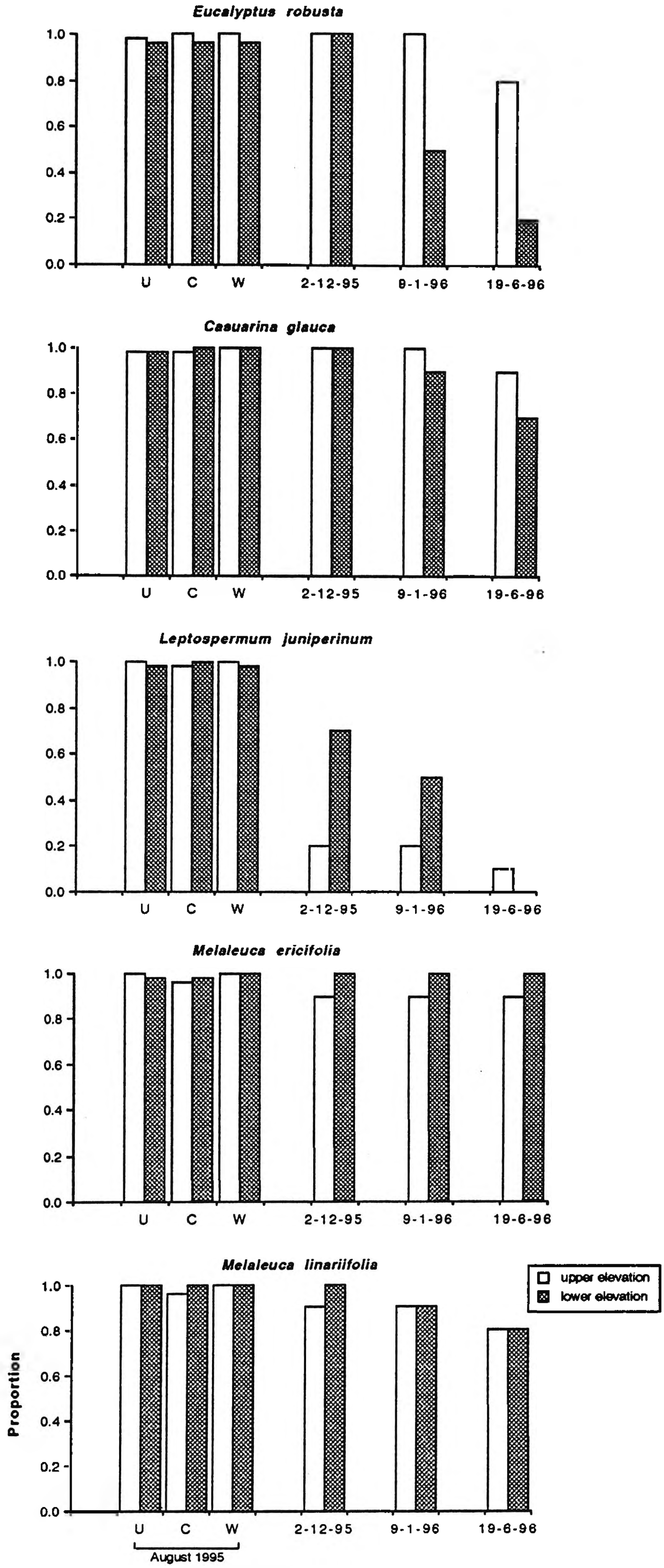


Figure 4.7 Survival of tubestock at intervals beween nine and twenty months after planting at two elevations in wet meadow. Tubestock were planted late Dec. '94 - Feb. '95. Plots: 'U' - uncleared; 'C' - cleared; 'W' - cleared & weeded. 'n' plots 50 ± 4.

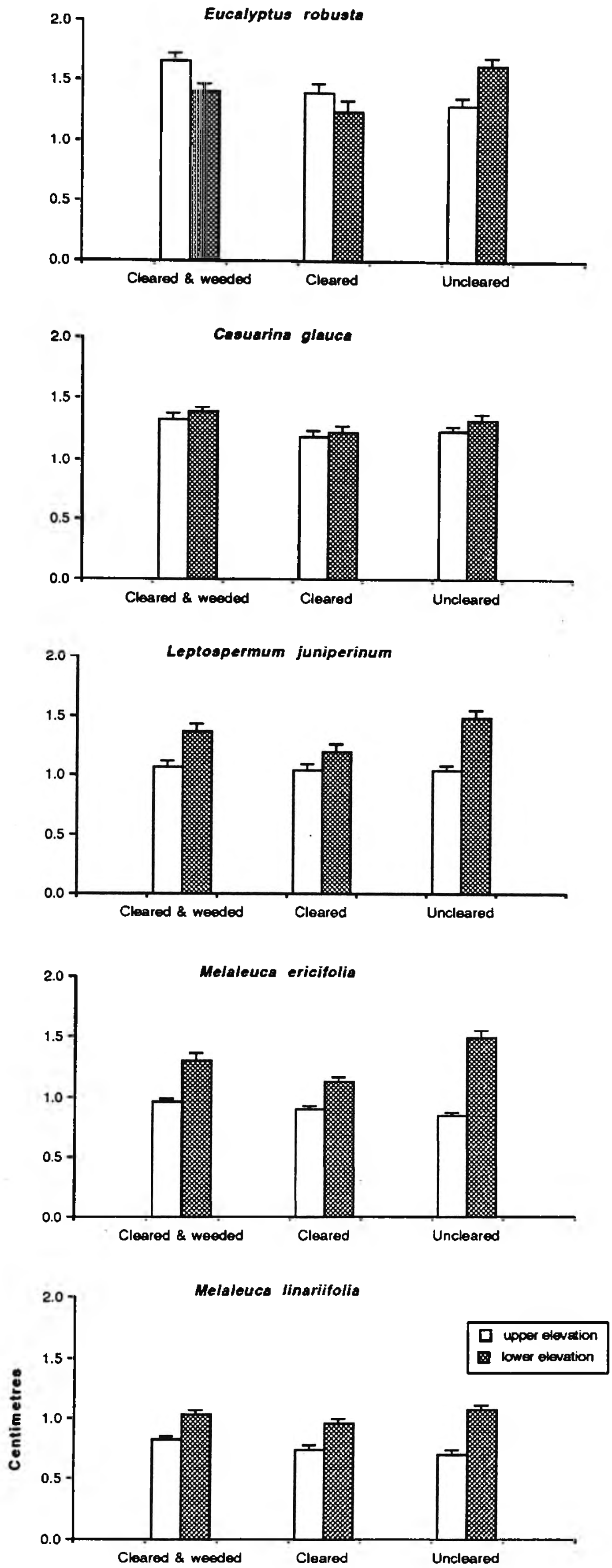


Figure 4.8 Stem diameters after nine months for tubestock of five woody species which received different treatments when planted into plots in wet meadow (see text). 'n' plots 50 ± 4.

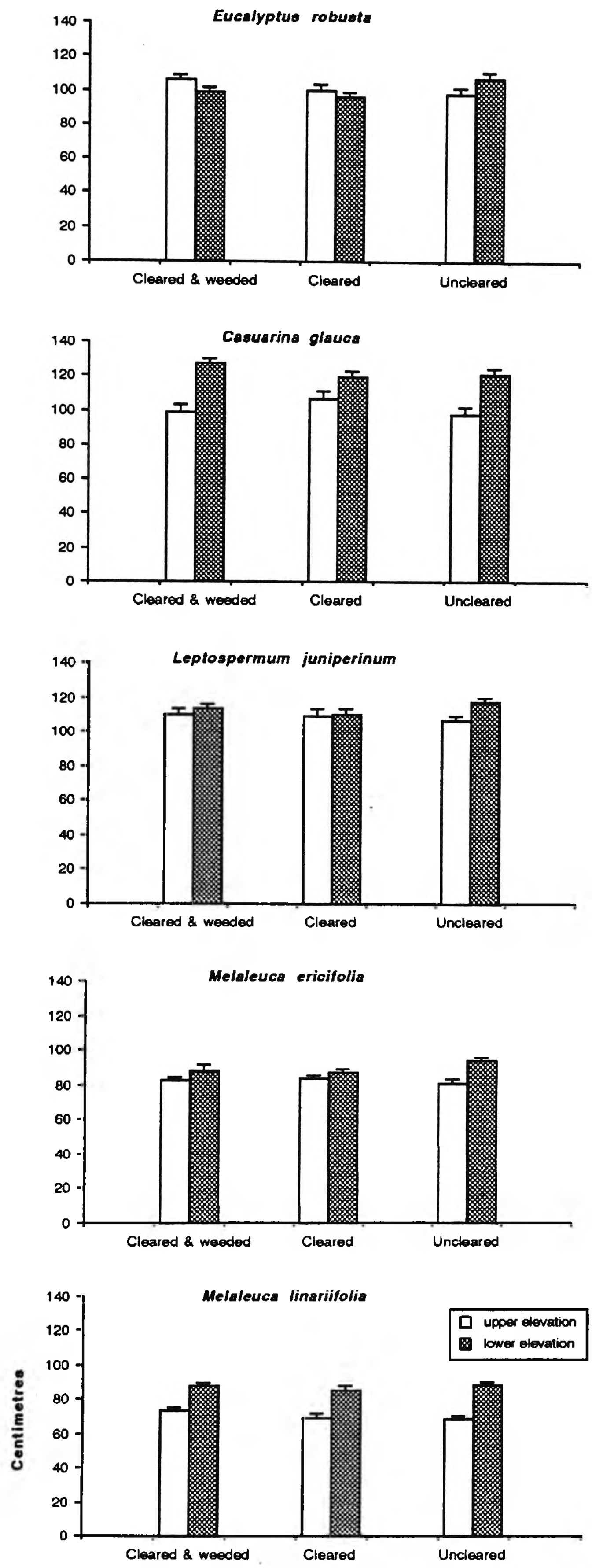


Figure 4.9 Heights after nine months for tubestock of five woody species which received different treatments when planted into plots in wet meadow (see text). 'n' plots 50 ± 4.

best in cleared and weeded plots. Statistical comparisons of stem diameter and plant heights after nine months at each elevation and among treatments are given in Appendix 11. Significant correlations of growth parameters with surrounding vegetation height were found only for *Eucalyptus robusta* and *Casuarina glauca* (upper planting) (Table 4.4).

Melaleuca ericifolia, Melaleuca linariifolia and *Casuarina glauca* (Fig. 4.10) showed good survivorship over a subsequent 11 months (Fig. 4.7) which included a long period of inundation (Fig. 4.2). Differences in stem diameter and height growth between upper and lower plantings for these species were no longer apparent after this time, but sample sizes were much smaller (Tables 4.5 & 4.6). However, plants of the latter two species exhibited signs of stress (leaf loss, fungal damage) at the lower elevation (pers. obs.). Few *Leptospermum juniperinum* and *Eucalyptus robusta* (at the low elevation - compare to Fig. 4.10) survived the wetter conditions.

The invasion of large, robust weeds into cleared plots was particularly pronounced in summer at the lower elevation planting (Fig. 4.11). Major invasive species included *Persicaria* spp., *Echinochloa crus-galli* and *Bidens tripartita.*

A number of *Eucalyptus robusta* and *Casuarina glauca* in the upper elevation planting were browsed, possibly by Swamp Wallabies, during the 1995 winter. At that time the lower planting was inundated. Browsing was reduced with an increase in water levels and all plants recovered.

All species developed long thin, laterally branching roots confined to the upper 20 - 50 cm of soil (Fig. 4.12). Saplings of all species survived one in twenty year winds which blew for four days (5-8th Nov. 1994). Many *Casuarina glauca* and *Eucalyptus robusta* plants were (and still are) growing

Table 4.4 Surrounding vegetation height and correlations with sapling height and stem diameter after nine months.

Species	Elevation	Surrounding vegetation height	Correlations with:	
			Stem diameter	Plant height
Eucalyptus robusta	upper	41 (2) (149)	0.23**	0.42***
	lower	39 (2)(141)	0.30***	0.33***
Casuarina glauca	upper	43 (2) (147)	0.10	0.41***
	lower	43 (2) (148)	0.07	0.14
Leptospermum juniperinum	upper	47 (3) (147)	0.09	0.18
	lower	53 (4) (149)	-0.01	0.10
Melaleuca ericifolia	upper	46 (3) (148)	-0.11	0.12
	lower	39 (1) (148)*	-0.05	0.08
Melaleuca linariifolia	upper	27 (2) (148)	0.09	0.15
	lower	66 (3) (150)***	-0.03	-0.02

Vegetation height in centimetres with standard errors followed by 'n' plots in parentheses. *Significant at $P < 0.05$; **significant at $P < 0.01$; ***significant at $P < 0.001$ (t-test - two tailed).

A

B

Figure 4.10 Saplings of: **A** - *Eucalyptus robusta*; and **B** - *Casuarina glauca* after 20 months growth at the upper elevation in wet meadow at Coomonderry Swamp.

Table 4.5 Mean stem diameters (cm) of saplings after twenty months.

Species	**Upper elevation**	**Lower elevation**
Eucalyptus robusta	3.35 (0.32) 8	1.68 (0.26) 2
Casuarina glauca	2.17 (0.14) 9	2.13 (0.24) 7
Leptospermum juniperinum	1.14 1	nil
Melaleuca ericifolia	2.68 (0.47) 9	3.08 (0.24) 10
Melaleuca linariifolia	2.44 (0.21) 8	2.90 (0.36) 8

Means for *Melaleuca ericifolia, Melaleuca linariifolia* and *Casuarina glauca* at upper and lower elevations respectively were not significantly different at $P = 0.05$ (t-test). Standard errors in parentheses. 'n' shown below means.

Table 4.6 Mean heights (cm) of saplings after twenty months.

Species	Upper elevation	Lower elevation
Eucalyptus robusta	140 (10) 8	122 (9) 2
Casuarina glauca	134 (5) 9	151 (14) 7
Leptospermum juniperinum	80 1	nil
Melaleuca ericifolia	122 (8) 9	123 (5) 10
Melaleuca linariifolia	109 (6) 8	114 (6) 8

Means for *Melaleuca ericifolia, Melaleuca linariifolia* and *Casuarina glauca* at upper and lower elevations respectively were not significantly different at $P = 0.05$ (t-test). Standard errors in parentheses. 'n' shown below means.

Figure 4.11 Robust weed growth in a cleared, lower elevation plot containing a *Leptospermum juniperinum* sapling.

Figure 4.12 Extensive lateral root growth on a *Eucalyptus robusta* sapling.

at an angle. During prolonged inundation, bark below water level became softer, thicker and spongy in all species. *Casuarina glauca, Melaleuca ericifolia* and *Melaleuca linariifolia* plants developed adventitious aerial roots.

4.2.3.4 *Natural regeneration*

There had been a substantial increase in the number of woody plants in the wet meadow region over the period 1994 - 1996. The sequence of photographs (Fig. 4.13a-d) clearly shows the rapidity of growth occurring in woody species. Figure 4.10b indicates that seeds of some woody plant species, particularly *Melaleuca ericifolia* and *Casuarina glauca,* had been dispersed some hundreds of metres from the undisturbed woody, wetland margin. Towards the latter period of sampling, *Casuarina glauca* saplings had been recorded along Transect 1 (Section 3.3).

Casuarina glauca plants were regenerating in greater numbers than other species and were generally restricted to elevations estimated to be inundated from 50% to at least 10% of the time (pers. obs. using Fig. 3.8). Numerous *Melaleuca ericifolia* plants had regenerated much closer to the wooded margin as a clump at the water margin. This clump, and the one visible in Fig. 4.10, may be clonal growths.

4.2.4 <u>Discussion</u>

Debate has recently arisen between leading researchers in the field of wetland restoration as to the outcomes to be expected once hydrologies have been 'rectified'. Two apparently incompatible hypotheses have been promulgated: (i) the 'designer' hypothesis (Galatowitsch & van der Valk 1996; van der Valk 1996) suggested that if only inundation regime is rectified, restorations will not necessarily proceed to the species

A

B

Figure 4.13 Natural regeneration in wet meadow adjacent to the undisturbed margin at Coomonderry Swamp. 'A' April 1994; 'B' April 1995. ...cont'd

C

D

Figure 4.13 (cont'd) Natural regeneration in wet meadow adjacent to the undisturbed margin at Coomonderry Swamp. 'C' January 1996; 'D' June 1996.

compositional equivalency of 'natural' systems; (ii) the 'self design' or 'efficient community' hypothesis suggests that rectification of hydrology through an understanding of 'wetland function' will, given time, result in successful restoration (Mitsch & Wilson 1996; Mitsch 1996). The term 'wetland function' is generally used in the wetland literature to refer to the regime of responses of species, communities and wetland systems to changes in abiotic and biotic processes, but is also commonly applied in discussions of hydrology alone.

As expressed here, these views represent extremes, each with their component dangers for wetland designers. Mitch and Wilson (1996) likened the former view to 'ecological gardening', the danger being that restoration is often considered successful because plants have survived over the short time when introduced into zones, but that desired species composition and function were often not achieved in the long term. Galatowitsch & van der Valk (1996) expressed concerns about the latter hypothesis because it failed to provide for establishment patterns and dispersal ability. Both Galatowitsch & van der Valk (1996) and Mitch and Wilson (1996) provided numerous examples of failed restoration attempts in support of their respective arguments. Concern for the failure of mitigation generally, had probably induced each of these workers to highlight different causes for restoration failure. In fact there is substantial agreement between Galatowitsch & van der Valk (1996) and Mitch and Wilson (1996) since both emphasize the need to restore hydrology and provide for establishment of all potential species.

Clearly, wetland function (in the full context) needs to be understood in order to adequately rectify hydrology. Indigenous wetland species may need to be introduced with the provision of appropriate establishment conditions where seedbanks are diminished or dispersal is low, and it must be understood that natural processes will determine the distributions and abundances of all species over time.

What are the implications of this debate for the present study? Firstly, it is apparent that in wet meadow at the southern end of Coomonderry Swamp, the natural regeneration of local woody plants has occurred following cessation of farming and the exclusion of cattle. The pattern of spread, with respect to the existing woody margin, and the length of time that wet meadow has been cleared, both suggest that recruitment occurs by dispersal rather than from an *in situ* seedbank. Coomonderry Swamp is an example of where I believe 'self design' and time would allow natural regeneration to occur because of the proximity of indigenous seed sources.

However, other degraded freshwater sites in the region are generally isolated from seed sources of most indigenous woody plants. With the exception of *Casuarina glauca* at Killalea wetland and Foy's Swamp, adjacent to Coomonderry Swamp, it is doubtful that time alone would allow recruitment of indigenous woody species once grazing, clearing or other land use had been curtailed. These wetlands require some 'design'.

It is important to consider that restored hydrology, the focus of the discussion of Galatowitsch & van der Valk (1996) and Mitch and Wilson (1996), is generally not the issue for these small wetlands (or at present for Coomonderry Swamp). For example, the pristine hydrologies of Jerrara Dam, Spring Creek Lake and Frog's Hollow, Bomaderry (Fig. 1.6) are either not known or the wetlands were constructed. Thus there are no *a priori* models, and managers are restoring these wetlands by minimising detrimental human impacts and replacing introduced grasses at the wetland margin with herbaceous wetland species and finally planting with indigenous woody species.

The experiment described in this section provided a number of insights, not only into the most effective (cost and time) planting procedures for five indigenous species at local wetland restoration sites, but also for woody plant restoration in general:

(i) Raising plants as tubestock required minimal effort. Seeds of all wetland woody species at Coomonderry Swamp could be easily collected. All, or almost all, seeds were viable and germinated readily, without treatment. Seedlings could be 'pricked' from seed trays and individually potted quickly (> 100 per hour). Under glasshouse conditions, seedlings were raised to a height appropriate for planting into existing vegetation within six months of germination.

(ii) Placing tube stock directly into uncleared vegetation was the most efficient and least environmentally damaging mode of restoration in wet meadow at Coomonderry Swamp. Hundreds of tubestock were able to be planted in a day by one person. In contrast, clearing plots of existing vegetation was extremely laborious and time-consuming. While weeding may have provided some early benefit to plants, at upper elevations, this advantage was not commensurate with the effort required. Unweeded saplings survived equally well. Sapling growth appeared to be inhibited in cleared plots at the lower elevation where weed invasion was more pronounced (Figs. 4.8 & 4.9). Cleared and unweeded plots at both elevations resulted in the least successful growth of saplings and provided the best opportunities for exotic weed invasion.

(iii) This study confirmed that natural patterns of vegetation (and regeneration) should be used as a guide to restoration. At Coomonderry Swamp, *Leptospermum juniperinum* was found on ground rarely inundated, while *Eucalyptus robusta* occurred higher on the elevation gradient than *Melaleuca ericifolia, Melaleuca linariifolia* and *Casuarina glauca*. The latter three species tolerated a broad range of inundation conditions, although *Casuarina glauca* appeared to be more frequent on dryer margins (Section 2.2). The survivorship and growth results from the planting experiment mirrored these natural patterns (Sectin 4.2.3.3).

(iv) Clearing plots for seeds or plants not only provided gaps for weed invasion but allowed thick algal growth and disturbed the acid sulfate soils.

(v) Inundation regime and consequent effects on soils (Hammer 1992; Mitch & Gosselink 1993) (rather than intrinsic differences between soils) were considered to have been the primary determinants of survivorship and growth at the two elevations. However differences in the micro-environment of plots were also found to be important for seed germination.

(vi) Planting with seed may only be a viable option for wetland creation in cleared sites and where water levels can be manipulated. It was unclear why regeneration was able to occur naturally within wet meadow, but was unsuccessful in uncleared plots in the experiment. Successful natural regeneration may be the consequence of very large numbers of seeds dispersed, coupled with the requirement for specific microsite conditions not encountered in the experimental planting.

4.3 Spatial variation and gap invasion within wet meadow at Coomonderry Swamp

4.3.1 Aims

To examine spatial variation in vegetation within wet meadow - a supplementary investigation to Section 3.2.

To investigate the relationship between surrounding vegetation and invasion of gaps by stoloniferous and rhizomatous species.

To investigate inundation regime and seasonal influences on weed vs indigenous establishment in gaps in wet meadow.

4.3.2 Methods

The analyses described in this section were constrained by the design and time requirements of Section 4.2.

4.3.2.1 *Spatial dynamics and gap invasion by vegetative spread*

The planting regions for *Eucalyptus robusta, Casuarina glauca, Leptospermum juniperinum, Melaleuca ericifolia* and *Melaleuca linariifolia* at each elevation were termed areas 1 - 5 respectively. Each of these areas were approximately 15 m x 20 m, and contained 300 plots of which 200 were cleared. Upper elevation and lower elevation areas corresponded to regions at about 50 m and 110 m along Transect 1 (Site 1) respectively (Figs. 3.2 & 3.13). Thus the upper elevation areas were above Transects 1a - e, in Fig. 3.5, while the lower elevation areas were located at the modal water's edge (approximately 40 m along the gradient shown in Fig. 3.5). It should be noted that both these elevations are within wet meadow as defined in Section 2.2.3.

Species adjacent to plots were recorded (i.e. in a region approximately 0.5 m radius from the centre of each plot). Where percentage cover for any species was estimated to be ≥ 10 %, this was also noted. After two months, vegetative encroachment ≥ 10 % by these neighbours into cleared plots was recorded.

4.3.2.2 *Inundation regime and seasonal influences on weed vs indigenous establishment in gaps*

Species which had established in plots from seed or other propagules were recorded. Staggered planting and subsequent rotation of plot checks and weeding (Section 4.2.2) provided 10 'first checks' from late December 1994 to early May 1995. Note that upper and lower elevation plots could be compared since they were checked at the same time (or within days of each other). These surveys were continued at subsequent weeding times in one area at each elevation for a further four months. This represented a record from the beginning of summer till the end of winter. At the beginning of the planting experiment (October 1994), upper plots were saturated and lower plots were inundated (Fig. 4.2), but then followed a long period of dryer conditions. In May 1995, lower plots were again inundated with upper plots at, or just above the water table. The inundation level thereafter remained relatively stable till late August 1995 (Fig. 4.2). Unfortunately the planting experiment described in Section 4.2 had to be scaled down at that time and this section of work could not be continued over spring.

4.3.3 Results

4.3.3.1 *Spatial dynamics and gap invasion by vegetative spread*

Spatial variation Only the five most prevalent species are shown in Fig. 4.14. It should be noted that some of these species were less prevalent,

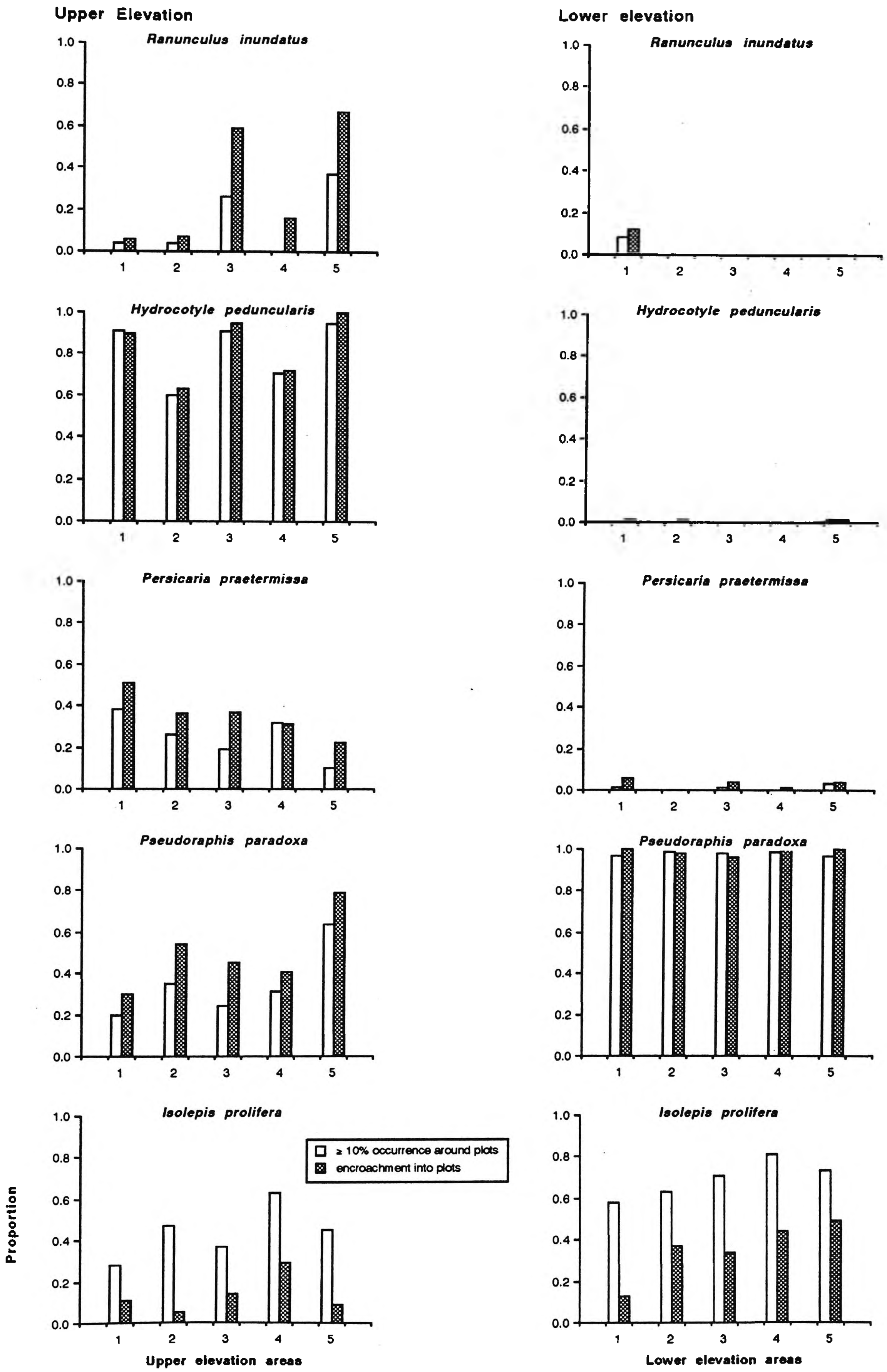


Figure 4.14 Occurrence around plots and encroachment into plots of five perennial herbaceous species at two elevations in wet meadow at Coomonderry Swamp. 'n' plots = 300 ± 2 and 200± 4 respectively (see Section 4.3.2.1).

and others more common, in winter (Table 3.5). The species shown were all perennials capable of stoloniferous or rhizomatous spread. Spatial variation in composition was greatest in the upper elevation areas. At the lower elevation there was strong spatial uniformity, with the dominants, *Pseudoraphis paradoxa* and *Isolepis prolifera* dictating vegetation structure.

Invasion of gaps by vegetative encroachment Species with the greatest abundance and distribution were those responsible for greatest encroachment into cleared plots. There was an obvious relationship between the prevalence of a species in an area and the prevalence of gap invasion by that species. At both elevations, *Isolepis prolifera* spread less rapidly into plots than the other four species. *Pseudoraphis paradoxa, Hydrocotyle peduncularis, Persicaria praetermissa* and *Ranunculus inundatus* showed strong infiltration of cleared plots even when not abundant adjacent to plots. Other species encroaching into plots, not shown in Fig. 4.14, are listed in Appendix 12.

4.3.3.2 *Inundation regime and seasonal influences on weed vs indigenous establishment in gaps*

The ten species shown in Fig. 4.15a - c represented the vast majority of individual plants which established within plot from seeds or other propagules (excluding vegetative encroachment). However, 43 other species sporadically occurred and these are listed in Appendix 12. Of these, 20 were exotics. Very small seedlings could not be identified and were not recorded.

It is clear from inspection of Fig. 4.15a - c that germination and establishment from seed was much greater in gaps at the lower elevation than at the upper elevation, and greater in autumn, moderate in summer and least in winter. Invasive 'weed' growth was also more robust in lower

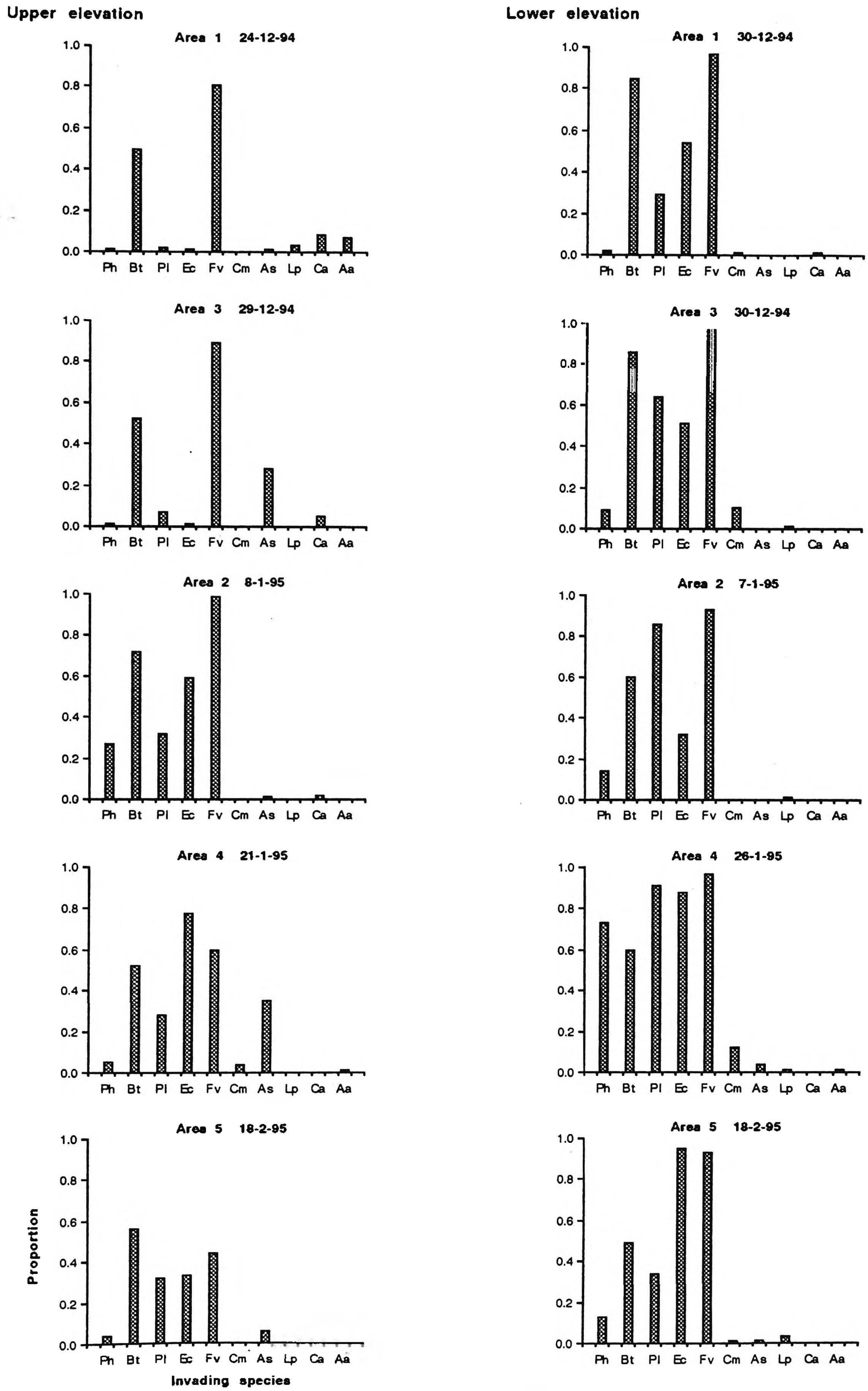


Figure 4.15a Summer germination and establishment of propagules in plots at two elevations in wet meadow at Coomonderry Swamp. 'n' plots = 100 ± 2. Initials represent species names: *Persicaria hydropiper, Bidens tripartita, Persicaria lapathifolia.* ...cont'd

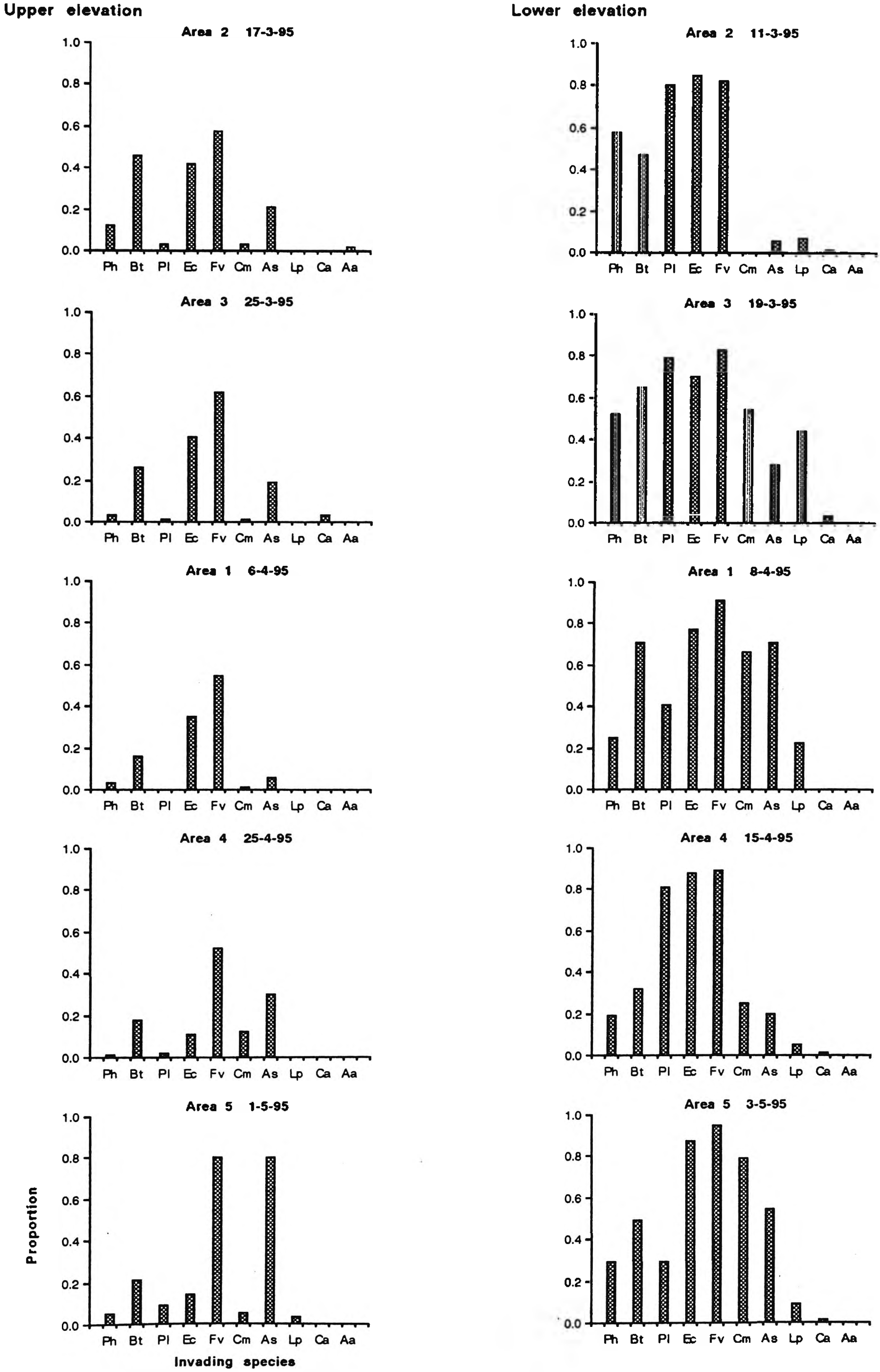


Figure 4.15b Autumn germination and establishment of propagules in plots at two elevations in wet meadow at Coomonderry Swamp. Species names continued: *Echinochloa crus-galli, Fimbristylis velata, Centipeda minima, Aster subulatus.* **...cont'd**

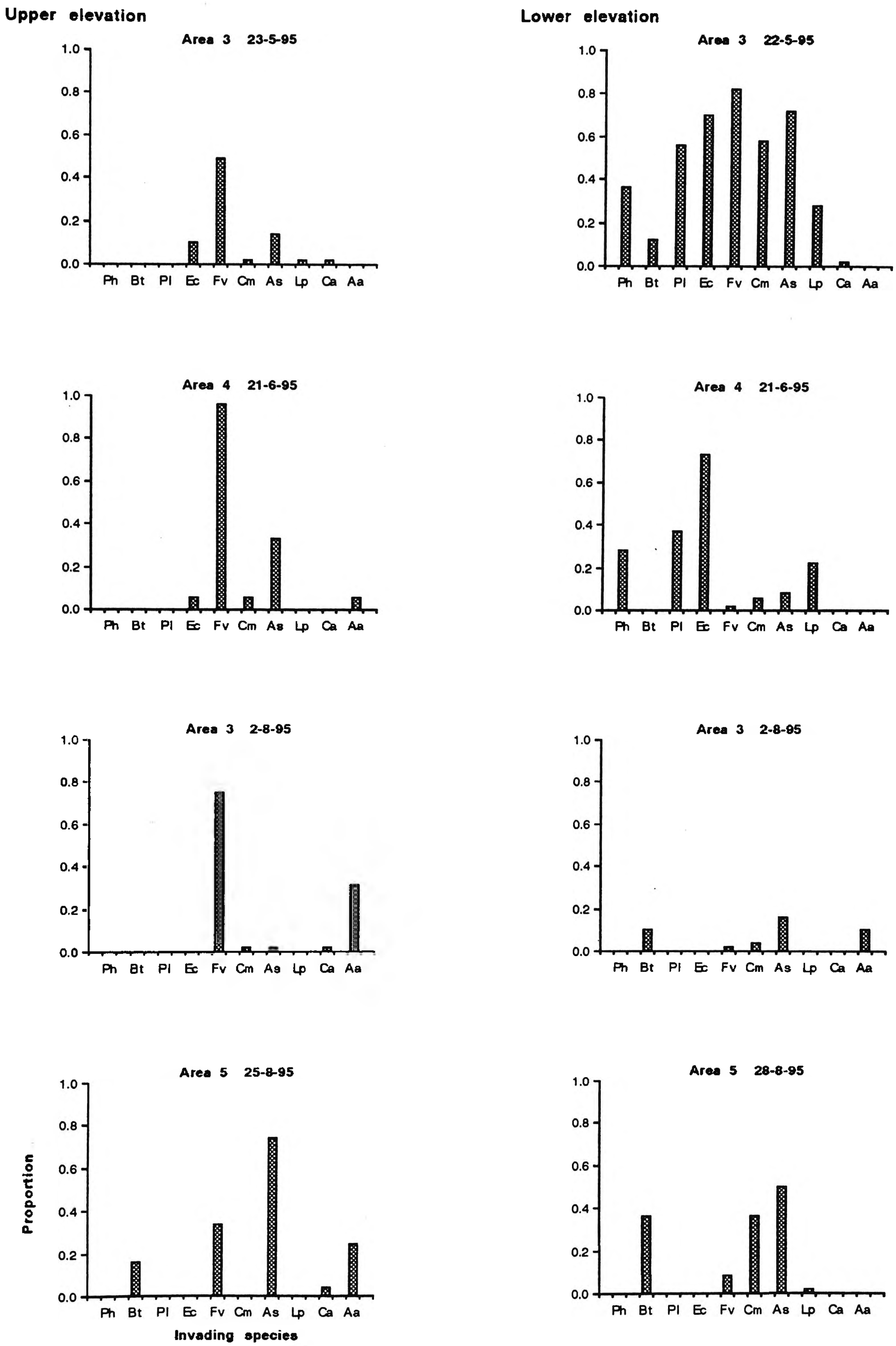


Figure 4.15c Autumn to winter germination and establishment of propagules in plots at two elevations in wet meadow at Coomonderry Swamp. Species names continued: *Ludwigia peploides, Conyza albida, Agrostis avenacea.* 'n' plots = 50 ± 1 (2nd & 3rd weeding visits).

elevation plots (compare Figs. 4.10 & 4.11). Three of the species responsible for extensive invasion into plots were exotics: *Bidens tripartita, Echinochloa crus-galli* and *Conyza albida.* Robust, large growing weeds included the aforementioned species and *Aster subulatus, Persicaria hydropiper* and *Persicaria lapathifolia.* Two smaller species, *Fimbristylis velata* and *Centipeda minima* were not previously recorded from wet meadow, but were strongly associated with ephemeral communities (Section 2.2.3.2).

4.3.4 Discussion

4.3.4.1 *Spatial dynamics and gap invasion by vegetative spread*

Spatial dynamics It needs to be remembered that both upper and lower elevation areas considered in this chapter were located within wet meadow and above the major transition to *Marsilea mutica* or mud communities which transiently occur lower on the elevation gradient. The spatial uniformity across lower elevation areas, dictated by the presence of *Isolepis prolifera* and *Pseudoraphis paradoxa,* corresponded to the equally strong, short term, temporal stability shown by these species at around 100 m in Fig. 3.13. In fact, Fig. 3.13 indicated why *Isolepis prolifera* was less strongly represented in Fig. 4.14. In all lower elevation areas there was a clear boundary (at the modal water's edge) above which *Pseudoraphis paradoxa* was, for a small segment of the gradient, a sole dominant, and below which *Pseudoraphis paradoxa* was still prevalent but *Isolepis prolifera* became increasingly important. Surprizingly, this visually distinct boundary (Figs. 3.14b & 3.17b) did not coincide with a community boundary defined by cluster analysis (Section 3.3.3.2).

The greater spatial variation among the upper elevation areas at the dryer end of the wet meadow transition are in agreement with a corresponding temporal flux (Fig. 3.13). However, temporal patch dynamics were never such that species were eliminated and compositional change result in community redefinition (Section 3.3.3.2) and it is considered that the degree of spatial change indicated in Fig. 4.14 is of no greater scale (thus confirming the findings of Section 3.2).

In fact, the differences between the upper elevation areas in the occurrence of dominant species around plots (Fig. 4.14) are suggestive of the type of fluctuating competitive interactions hypothesised for these same species in Section 3.4. Furthermore, *Isolepis prolifera* was least prevalent in dry spring-summers following wet winters (Figure 3.13) and these were the conditions experienced for the present investigation. I consider that as a consequence of this decline in *Isolepis prolifera,* the other species shown in Figure 4.14 had greater abundances and distributions.

Gap invasion by vegetative encroachment Gaps are not common in wet meadow at Coomonderry Swamp. They may occur in winter time at upper elevations with senescence of some species: *Persicaria* spp., *Pseudoraphis paradoxa,* various annuals, especially *Bidens tripartita, Echinochloa crus-galli* and *Aster subulatus,* and to some extent *Isolepis prolifera;* but generally, space where vegetative invasion occurs is still well covered with plant biomass. Small scale vegetative plant dynamics is thus more a consequence of fluctuating competitive abilities (Section 3.4.4). In habitats such as these, it may well be that species reliant on rhizomatous spread would be more disadvantaged by competitive exclusion than species capable of stoloniferous proliferation. While all the species shown in Fig. 4.14 are stoloniferous, *Isolepis prolifera* is an erect species capable of proliferating from spikelets. Such a growth form might preclude fast invasion of gaps (Fig. 4.14), but probably allows better spread across existing biomass.

Brewer and Bertness (1996) investigated a number of aspects of 'clonal mobility' in salt marsh. In particular, they commented: (i) on the more efficient gap colonization of poor competitors, (ii) that harsh conditions in gaps could be facilitated by physiological integration with ramets located outside gaps, and (iii) that intraspecific variation in rhizomatous gap invasion probably occurred in some species at some sites (i.e. greater clone mobility in dense swards). These would all be interesting hypotheses to test for the clonal species which dominated the wet meadow vegetation at Coomonderry Swamp (in a differently designed experiment c.f. Brewer and Bertness 1996). While clonal invasion was investigated at two elevations in the present study, both were in dense vegetation and there was no evidence of intraspecific variation. Differences might be found if comparisons were made with these species where they occur in more harsh conditions i.e. lower still on the elevation gradient.

4.3.4.2 *Inundation regime and seasonal influences on weed vs indigenous establishment in gaps*

Numerous studies have investigated factors influencing establishment success of propagules in wetland environments. Inundation regime and biotic interactions are integral components (e.g. Wilson & Keddy 1986b; van der Valk & Davis 1988; Welling *et al.* 1988; Keddy *et al.* 1994; Bonis *et al.* 1995; Gaudet & Keddy 1995; Weiher & Keddy 1995a & b), but other factors have been shown to be important at some sites. These include organic content (e.g. Wilson & Keddy 1985, 1986a & b); soil moisture and water quality (Smith & Kadlec 1983); life form traits (e.g. Shipley *et al.* 1989; Bonis *et al.* 1995; Weiher & Keddy 1995b); fertility and leaf litter (e.g. Weiher & Keddy 1995a); and seed size & soil particle size (e.g. Keddy & Constable 1986).

Seasonal effects must also be considered as an integral component determining propagule success, but fewer studies have dealt with the issue (Thompson & Grime 1983; Baskin *et al.* 1989; Yen & Myerscough 1989a &b; Britton & Brock 1994). The impetus for the present survey arose from the recent work of Britton and Brock (1994) who showed that wetland plants of the NSW northern tablelands showed the least amount of germination (both individuals and species) in summer. They argued that wetland plants may have locally evolved a sensitivity to a combination of high maximum and minimum temperatures which inhibited germination. Britton and Brock (1994) saw predictable temperature as a reliable cue in a region where wetlands experienced unpredictable inundation.

Britton and Brock (1994) referred to the work of Baskin *et al.* (1989) who argued that wetland plants generally, from regions with unpredictable water regimes, could germinate at most times in the growing season and over a wide range of temperatures. They also referred to the study of Thompson and Grime (1983) who showed that predictable temperature variations in the British spring coincided with predictable inundation conditions which were conducive to wetland plant germination and establishment. Thus British wetland plants may have evolved a sensitivity to temperature as an indicator of favourable conditions. The question was: how important was season in determining germination at Coomonderry Swamp?

Inundation regime at Coomonderry Swamp appears to be unpredictable in the sense that (i) drawdowns or flooding may occur in any season and may be of any duration, and (ii) water levels respond rapidly to rainfall events. Yet there is less seasonality in temperature. At Jervis Bay, the nearest coastal meteorological centre, mean maximum and minimum temperatures range from 24.1 and 18.0 respectively in February to 15.2 and 9.0 respectively in

July (Bureau of Meteorology records). Thus temperature at Coomonderry Swamp would be a much more subtle cue (albeit predictable) and the chances of desiccation much less frequent than in wetlands of the northern tablelands of NSW. Furthermore, gaps did not commonly occur in wet meadow where existing vegetation pre-emptively excluded most establishment from seeds (but with some notable exceptions e.g. regeneration of woody plants - Section 4.2.3.4). The best chances for germination and establishment, particularly for transient opportunists, occurred lower on the elevation gradient during drawdowns.

It was not expected that the incomplete record shown in Fig. 4.15a - c would provide any definitive answer to the question of seasonality and germination but would provide indicators to the generation of further hypotheses. It did appear that under the prevailing conditions, the number of individuals and species germinating in autumn was greater than in summer. The winter data need to be treated with greater caution since they represented second and third weeding visits and seedbank depletion may have been substantial. Based on this limited data I suggest, as a working hypothesis (and in agreement with Baskin *et al.* (1989)), that most species at Coomonderry Swamp are capable of germination and establishment throughout the year and that germination is neither inhibited nor promoted strongly by temperature cues. Nevertheless, for most species there is a definite growing season (spring to autumn), and species obviously show strong phenological responses at other life stages and for other reasons. I also suggest that drawdowns are critical events for opportunist species to replenish seedbanks, not only *in situ,* but by dispersal, over much wider areas, including the wet meadow where establishment events may be rare.

The fewer germinations at upper elevations is interesting and there are a number of possible explanations: (i) wetland plant seeds may germinate and establish better in saturated rather than moist soils; (ii) prolonged saturation may be required to break the dormancy of some species and (iii) vegetative encroachment appeared to be more rapid in upper elevation areas and germination and establishment may have been competitively reduced. These possibilities require further investigation.

While drawdowns are necessary for the replenishment of some indigenous seedbanks (note particularly the success of *Fimbristylus velata* in gaps), they also provide a seed source, together with adjacent pastures, for a large number of introduced species, many of which are considered serious weeds.

4.4 Summary

4.4.1 Establishment of indigenous woody species within coastal, freshwater wet meadow

(i) Coomonderry Swamp is the only available reference site for freshwater wetland restoration in the Illawarra and Shoalhaven regions of NSW.

(ii) There is a growing demand for published information on the ecology of woody wetland plants. Planting of woody species within existing herbaceous vegetation on the margins of wetlands is an integral part of most coastal wetland restorations in NSW.

(iii) Using tubestock raised from locally collected seed, and planted directly without disturbing existing vegetation was a practical and cost efficient method of restoration.

(iv) *Casuarina glauca, Melaleuca ericifolia* and *Melaleuca linariifolia* all grew well when planted directly in wet meadow at both upper and lower elevations at Coomonderry Swamp. *Eucalyptus robusta* survived better at upper elevations, while *Leptospermum juniperinum* did not succeed at either elevation planting. The latter species is considered to prefer soils less frequently inundated.

(v) Natural distributions and patterns of regeneration are an important guide to appropriate planting elevations for these indigenous woody species.

(vi) Minimizing disturbance during planting reduced the amount of weed growth.

(vii) Soils with acid sulfate potential may be close to the surface in coastal wetlands and may be exposed if soils are disturbed during planting.

(viii) While there was evidence of natural regeneration, direct seeding into existing vegetation, or cleared plots, was not found to be successful as a means of restoration. Direct seeding may be successful in newly created sites where weeds can be minimized and water levels manipulated.

4.4.2 Spatial dynamics in wet meadow

(i) This survey confirmed earlier findings (Section 3.2), that despite fluctuations in individual species distributions and abundances, there was spatial uniformity in species composition within wet meadow at the southern margins of Coomonderry Swamp.

4.4.3 Vegetative encroachment into cleared plots in wet meadow

(i) The most prevalent species were those most successful in invading cleared plots.

(ii) *Isolepis prolifera* was slower to spread into cleared plots than other species. However, its proliferating growth is considered to provide a competitive advantage in existing vegetation. There are few gaps normally in wet meadow.

(iii) The ability of *Pseudoraphis paradoxa, Hydrocotyle peduncularis, Persicaria praetermissa* and *Ranunculus inundatus* to spread into gaps even when not abundant adjacent to them again indicates the importance of competition in dictating composition and structure in wet meadow (Section 3.4).

4.4.4 Inundation regime and seasonal influences on weed vs indigenous establishment in gaps

(i) Forty four identified species established in cleared plots from propagules (non-vegetatively) over nine months, summer to winter. Twenty of these were introduced species and many are described as pests (Sainty & Jacobs 1981).

(ii) Availability of gaps, i.e. during drawdowns, is thought to be important to the local survival of some indigenous species. *Fimbristylus velata, Cyperus sanguinolentus, Centipeda minima, Isolepis fluitans* and *Triglochin striatum* were found in cleared gaps, but rarely, or never occurred in wet meadow.

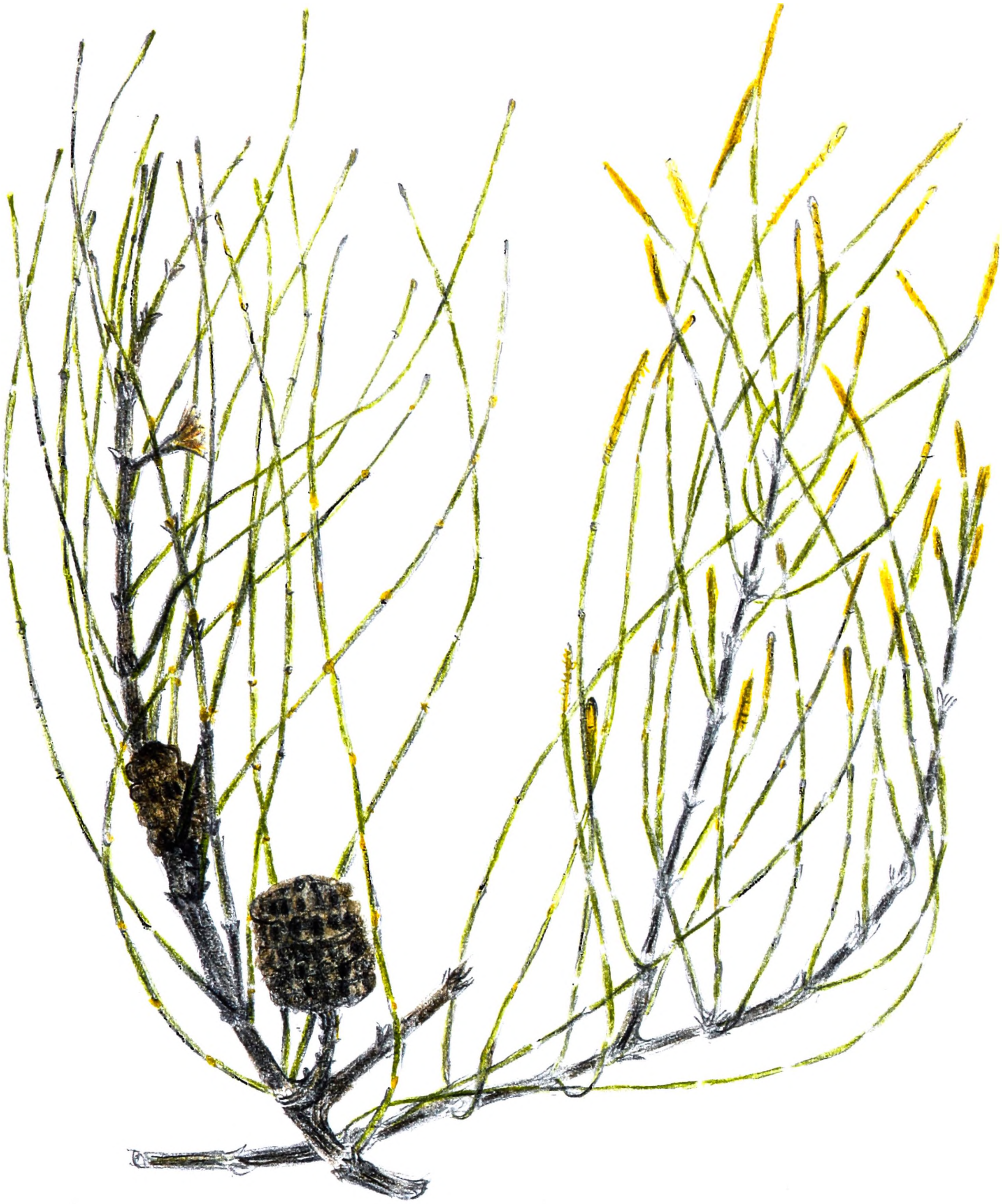
(iii) While greatest numbers of species and individuals established from seeds or other propagules in gaps in autumn and least in winter, the results were far from conclusive, and further studies will be needed to test the importance of season in determining recruitment for freshwater wetland species in this region.

4.5 Conclusion

Margins of most undisturbed wetlands on the south coast of NSW are predominantly wooded. Rehabilitation and re-establishment of buffer vegetation around wetlands that are degraded are major points in the wetland management policy of the NSW Government (Department of Land & Water Conservation 1996). Yet there is little information available on the propagation biology and ecology of indigenous woody species.

In this chapter I have shown that five common NSW wetland species can be easily propagated from seed and planted with no additional preparation into existing herbaceous vegetation. I have argued that local natural distributions provide a strong guide to the appropriate planting elevation, and that undue soil or vegetation disturbance can have deleterious effects.

Of course, a single field study must be viewed in context, but may nevertheless be of greater value than manipulated experiments which fail to emulate the full range of natural conditions. The planting procedures described will need to be tested at other sites. The additional benefit of field experiments and restoration is that they provide further opportunities to add to, and record, information on aspects of wetland function.



Casuarina glauca

Chapter 5 General Discussion

5.1 Introduction

There are eight important wetland sites on the Illawarra - Shoalhaven coastal plain (Australian Nature Conservation Agency 1996). All are under immediate or future threat (e.g. removal of peripheral vegetation, nutrient run off), since the region consistently boasts one of the fastest population growths in NSW. Six sites are predominantly estuarine. For two of these, Woolumboola Lake and St Georges Basin, estuary management plans have been prepared in keeping with the NSW Government Estuary Management Policy (NSW Gov. 1992; Shoalhaven City Council 1996b & c). However, both these waterbodies and a third, the Shoalhaven/Crookhaven estuary, require independent ecological investigation. The Jervis Bay area supports peripheral estuarine wetlands and some small associated freshwater bodies which are protected under RAMSAR. It has been the subject of much political and scientific attention in recent years (Ch. 1). Lake Illawarra, and the Minnumurra estuary have also previously been studied (Ch.1).

Killalea Lagoon and Coomonderry Swamp are geographically isolated examples of dunal, freshwater wetlands, although the former is small and extensively degraded. In contrast, Coomonderry Swamp at 670 ha, is probably the largest isolated dune contact wetland in NSW (ANCA 1996). It is relatively unspoiled, well vegetated because of its shallow depth, and is known to support a significant avian population. Yet it too has only received superficial scientific attention.

Since saltmarsh and mangroves of the south coast are, at least in a general sense, well studied (e.g. Clarke & Hannon 1967, 1969, 1970, 1971; Adam 1981a & b; Adam 1990; Adam & Hutchings 1987; Adam *et al.* 1988; Carne 1989;

Clarke 1993; Mitchell & Adam 1989a; Yassini 1985) and important estuarine sites are now subject to management planning, Coomonderry Swamp was an obvious, almost an imperative choice for this research.

With so little known about the floristics of Coomonderry Swamp, and most south coast wetlands generally, it was the intention to begin with a description of the pattern of vegetation (Ch. 2) and to progress to a preliminary understanding of the process of community change in response to hydrology and other key determinants of change (Ch. 3), and hence to an examination of the ecology of some key wetland species (Chs. 3 & 4). Pivotal works in wetland science (and these have been cited throughout this thesis) have emphasised the role of these three areas of research in conservation, management and restoration.

There are four objectives to the following discussion: (i) to review the contributions this research makes in the aforementioned three areas; (ii) to outline directions of continuing research and investigations which would complement the present study; (iii) to describe some endeavours at other Australian wetland research centres which would have particular value if implemented in the local region and (iv) to address the criteria for identifying wetlands of international importance (e.g. ANCA 1996) to Coomonderry Swamp to indicate its suitability to be listed as a Ramsar wetland.

5.2 The Research Contribution

Conservation of biodiversity is a major global challenge (Commonwealth of Australia 1996; NSW NPWS 1997) and was the unifying goal of this research. The comparison of Coomonderry Swamp with other wetlands defined its significance in a regional context and its floristic values for conservation. The research into spatial and temporal vegetation dynamics provided a baseline for monitoring future change to Coomonderry Swamp. Little work on woody plants for wetland restoration had previously been available and the techniques of germination and establishment developed for the five important species chosen, should be useful to wetland managers nationally.

Some aspects of the work on wetland processes and restoration had implications for wetland research beyond the regional scale. Examples included the work on cyclic patterns of vegetation change, pre-emptive competition in mesic environments and facilitation in harsh conditions, cost effective planting, the relative roles of seed and clonal growth in revegetation, and the role of fluctuating water regimes in plant establishment. The specific contributions of the research are detailed below.

5.2.1 Floristics and community description Plant species composition and communities were comprehensively described for three wetlands: Coomonderry Swamp, Killalea Lagoon and Werri Lagoon, a small estuarine system equidistant between the two freshwater systems. Detailed attention was given to Werri Lagoon because it supported an unusually complex saline wet meadow. Preliminary surveys were carried out at a further six wetlands to provide comparison to the principal reference site, Coomonderry Swamp.

A diverse range of plant communities was found at Coomonderry Swamp (Fig. 5.1) because composition and structure were determined by a complex interaction of factors. Principally, these were elevation and drainage with component effects on soil nutrient status, and disturbance and stress derived from anthropogenic influences and/or from flux in water levels. Surveys at the other eight wetlands resulted in identification of only one other factor (salinity) differentiating vegetation, and only a further four community

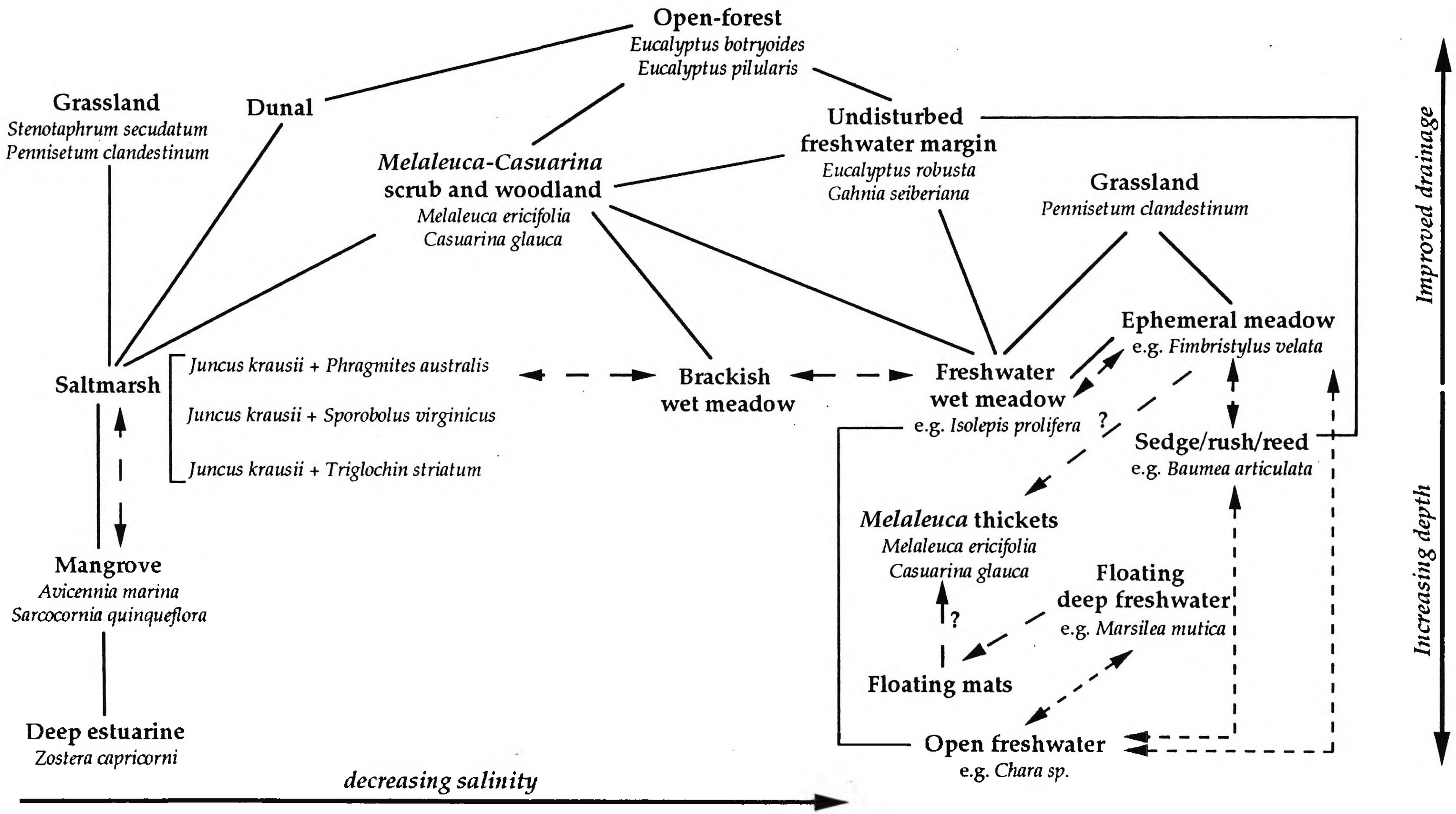


Figure 5.1 The influence of hydrology and salinity in determining plant communities at nine wetlands on the South Coast of NSW. Plain lines show common spatial transitions (zonations). Short dashed lines show observed short term temporal transitions. Longer dashed lines indicate some potential longer term changes. All community types, except brackish wet meadow, saltmarsh, mangrove and deep estuarine, were found at Coomonderry Swamp.

types: brackish wet meadow, saltmarsh, mangrove and deep estuarine. Wet heath communities were not surveyed (see Cho *et al.* 1995).

Some interesting aspects of community structure shown in Fig. 5.1 require mention. *Melaleuca ericifolia* and *Casuarina glauca* commonly occurred above the margins of almost all wetlands surveyed. Substantial stands of the *Eucalyptus robusta - Gahnia sieberiana* community type were restricted to Coomonderry Swamp. The cyclic dynamics at lower elevations observed at both Killalea Lagoon and Coomonderry Swamp, follow a pattern which is general to many freshwater wetlands (van der Valk 1981). It is hypothesized that *Melaleuca - Casuarina* thickets located in the deepest parts of Coomonderry Swamp may develop from floating mats (succession in floating marshes have been described by Sasser *et al.* 1996). An unlikely alternative is that extremely long drawdown events allowed these stands to develop on mud.

Some community types found at Coomonderry Swamp are regionally, perhaps nationally rare, e.g. *Eucalyptus robusta* freshwater margin and littoral rainforest. Others are of high value to fauna. In particular, Coomonderry Swamp, together with the extensive Shoalhaven - Crookhaven estuary, forms an important breeding and refuge site for avifauna (Blachford & Reeks 1976; Lawler & Porter 1990).

Two hundred and eleven plant species were recorded at Coomonderry Swamp during this study. These included 17 rare, regionally rare or poorly conserved species or hybrids, two protected species, and 17 species or hybrids at, near or beyond their previous known range, or newly recorded in the ecogeographic region (Harden 1990-93; Benson & McDougall 1993-95; Mills & Jakeman 1995). Five species recorded with extended known ranges were exotics. A further 88 species were recorded at the other eight wetlands surveyed, including an additional five rare, regionally rare or poorly conserved species and some well beyond previously recorded ranges.

5.2.2 Vegetation dynamics at Coomonderry Swamp The fifty year aerial photographic record indicated that Coomonderry Swamp had robustly withstood concerted attempts at drainage. The size and shape of the wetland had changed little over that time and broadscale vegetation patterns have not altered. Unfortunately, almost all other wetlands of the Shoalhaven and Crookhaven alluvial plain had been drained following European settlement.

Detailed investigation of vegetation dynamics was carried out in a portion of Coomonderry Swamp dominated by herbaceous vegetation. Two communities had previously been defined by cluster analysis: wet meadow in a region periodically inundated and a *Marsilea mutica* deep water community. The division between these two communities, located below the modal water's edge was shown to be relatively discrete, both spatially and temporally. Another boundary at the modal water's edge, indicated by a *Pseudoraphis paradoxa* - *Isolepis prolifera* transition, was equally distinct visually, but was not differentiated by cluster analysis.

Temporal analysis indicated little compositional change in the wet meadow community over 3.5 years of record, although some individual species showed marked variation in distribution and abundance in response to flux in inundation and/or season. The photographic record tended to over-emphasise these changes, while the constancy of dominant species and the inertia of the system, limited the ability of cluster analysis and ordination to detect dynamics.

The stability of the wet meadow community over time, the closed cover of the herbaceous canopy, the more benign conditions, and the predominance of negative pairwise species covariances suggested two hypotheses. Firstly, pre-emptive competition may minimize the opportunities for substantial change. Secondly, varying competitive abilities in response to changing conditions may be responsible for the observed dynamics in individual species distributions and abundances. Covariance data also suggested that there was some amelioration of competition between species via vertical partitioning of resources related to life form.

Communities were less stable at lower elevations, in keeping with more extreme fluctuations in water level. The *Marsilea mutica* community alternated with ephemeral mud communities, which in turn developed into stands of tall emergents when reflooded. The similarity of these cyclic alternations to the qualitative Gleasonian model of van der Valk (1981) was discussed in Section 3.3.4.2. Competition is hypothesised to be less important in determining floristic composition at lower elevations of the wet meadow transition because of the greater flux in inundation and the resulting transience of communities. In contrast, there was some evidence that wind/wave disturbance was ameliorated for some floating species by the presence of *Marsilea mutica*. *Marsilea mutica* may have been facilitated in turn by emergent stands of *Philydrum lanuginosum* and *Typha orientalis* in even deeper water.

In the introduction to Chapter 3, some questions pertaining specifically to temporal vegetation dynamics were posed. These questions, with summarized answers, are presented in Table 5.1.

5.2.3 The ecology of wetland plant species

Wetland ecology is a relatively new science and botanists have historically concentrated on taxonomy and distribution. Hence there are few books or manuals which summarize the ecology of a range of wetland species in a

Table 5.1 Answers to some questions posed in Chapter 3 which relate to temporal vegetation change at Coomonderry Swamp.

Questions	Summarized answers
How significant are the temporal variations in community attributes - do communities change through time?	There was little change over 3 years in either woody species or herbaceous understory species along the undisturbed margin. In wet meadow, individual perennial species fluctuated in abundance and distribution and there were a number of transient species. However species richness and overall composition did not vary sufficiently to allow a 'new' community to be defined using the criteria applied. Lower on the elevation gradient, inundation changes were more pronounced. Plant species' compositional change was such that two main communities were identified: a *Marsilea mutica* deepwater complex and an ephemeral mud community.
Can edaphic factors determining changes in vegetation be identified?	Cluster analysis and ordination had limited success in separating temporal samples on the basis of either inundation or seasonal change. This was due to the resilience of dominant species and the general inertia of the system. However community change was strongly correlated with the 'inundation index', a measure which averaged the period of inundation and number of fluctuations over 3 years. Direct gradient analysis of temporal samples illustrated the responses of individual species to changing season and inundation. Photography probably over-emphasized vegetation responses.
Can cyclic vegetation change be predicted from the application of a simple model?	Yes, at lower elevations community dynamics were consistent with van der Valk's (1981) cyclic model of wetland change. At higher elevations, no cyclic or directional patterns of change were recorded during the 3.5 years of this study.
Can significant interspecific interactions be identified?	Most correlations were not significant, although there were notable exceptions (Fig. 3.23). Measures of pairwise covariance were made in the context of a multispecies mix at a single site.
Do species pairwise interactions vary through time?	Most pairwise correlations were temporally constant. Most were negative, suggesting niche separation, competitive fluctuation or competitive exclusion. Some positive correlations suggested common responses to resources and others facilitation.
Is there support for the model of Bertness and Callaway (1994)?	Yes, there was some evidence to suggest that competition (N.B. pre-emptive) was more important at the mesic wet meadow end of the transition and that facilitation had a greater role at the lower end of the gradient where conditions were more extreme.

form which is useful to wetland managers and restorers (but see Grime *et al.* 1988; Hammer 1992; Chambers *et al.* 1995). In this research, information accumulated from the wetlands surveyed (Ch. 2) and from the analysis of dynamics (Ch. 3) have been used to compile ecological profiles of 15 key herbaceous species (Table 3.5). Potentially, the ecology of many more species could have been profiled using the type of information available in Chapters 2,3 and 4 (e.g. Figs. 2.14, 3.13 & 4.15, Tables 2.1, 2.4,2.5,3.3 & 3.4, and Appendices 5,6 & 7) and unpublished data. Of course, the ecological profiles in Table 3.5 need to be supplemented by measurements of more parameters for each species over a broader range of habitats (Ch. 5.3).

The initial impetus for ecological profiles arose from the need to provide a better procedure for delineating wetland boundaries (Adam *et al.* 1985; Adam 1992). In particular, where herbaceous wetlands abut agricultural land, boundaries are difficult to define. It had been hoped that species, or suites of species, might be identified that would have some general function in identifying these upper boundaries. However, the temporal and spatial surveys carried out at Coomonderry Swamp and surveys at other wetlands did not suggest species ideally suited to the purpose. In my view, where development or altered rezoning is intended, wetland boundaries and buffer zones will need to be determined in the field on a site-by-site basis. This will involve the identification of truly aquatic species on organic soils and buffer zone species on humic soils which may well be specific to the site in question.

Nevertheless, understanding the ecology of key species is important for other reasons. It is fundamental to: (i) the management of existing systems potentially subject to nutrient, hydrologic or other changes; and (ii) the restoration of degraded sites. In the former case, knowing the baseline conditions in a wetland, understanding the tolerances of key indigenous species to changes in hydrology or soil characteristics and finally, being aware of the likelihood of invasion by unwanted species, is important for optimal planning. In the latter case, information on the ecology of recruitment and establishment life phases is needed.

The need to provide information on the establishment of indigenous woody species was addressed in Chapter 4. The five species chosen - *Eucalyptu robusta, Casuarina glauca, Melaleuca ericifolia, Melaleuca linariifolia* and *Leptospermum juniperinum* - were all easily raised from locally collected seed, raised as tubestock and successfully planted without disturbance to existing soil or vegetation. Planting directly with seeds into existing vegetation was unsuccessful despite the evidence of natural regeneration by the same species. For the site chosen (degraded wet meadow at Coomonderry Swamp), clearing and weeding of plots proved to be a time-consuming and damaging practice. Plant growth was not improved in cleared, or cleared and weeded plots, and cleared plots allowed the establishment of weeds into the meadow vegetation.

During the course of the planting experiment, further data were accumulated on spatial dynamics and invasion of gaps within wet meadow. For example, vegetatively reproducing herbaceous species were found to vary in their ability to encroach into cleared gaps and some seasonality occurred in the numbers of individuals and species establishing in gaps from seed.

5.3 Directions of continuing research

In Chapter 1 I argued that, apart from some notable exceptions (i.e. Lake Illawarra and Jervis Bay), there had been little previous investigation of the vegetation ecology of south coast wetlands. Hence, despite the contributions described in Section 5.2, there are some important directions of research which need to be continued to ensure adequate conservation of the biological diversity in wetlands on the NSW South Coast.

The value to predictive ecology of pursuing temporal studies over the long term (i.e. > 5 years) has been emphasized by several researchers (e.g. PERL 1990; Mitch & Wilson 1996; Simenstad & Thom 1996; van Groenendael *et al.* 1996). For example, the complex model of community change presented in Figure 5.1 will have greater benefit regionally, and on a wider scale, if additional temporal data are accumulated which allow better definition of the causes of change (i.e. replication of hydrological events including extreme flooding and drawdown).

In this section I indicate some descriptive work which would augment the present study, briefly describe temporal investigations it would be beneficial to continue and suggest faunal surveys which would complement the floristic research completed at Coomonderry Swamp.

5.3.1 Identification of communities and floristics

The floristic surveys at Coomonderry, Killalea and Werri wetlands were comprehensive. It is expected that only a few additional ephemeral species will be identified. At the other six wetlands surveyed, most community types will have been identified but some areas were not traversed and more species await listing. A number of other wetlands in the Illawarra and Shoalhaven regions require floristic description. Investigation of the wet heath habitats, which occur around the periphery of Jervis Bay, was beyond the scope of the present research. It will be important to reapply these studies by including wet heath and adjoining swamp communities in the pattern analysis.

5.3.2 Vegetation dynamics

The baseline vegetation dynamics have now been established. Both transects within herbaceous vegetation and along the undisturbed margin will be revisited over the longer term. The prediction of a cyclic pattern of change at lower elevations, and of resilience of wet meadow, will need to be further investigated. Given the baseline data, substantial nutrient or hydrologic alterations to Coomonderry Swamp should now be able to be detected along with longer term directional changes in plant community structure and composition.

5.3.3 Woody plant restoration

At this point in time (after 24 months) sapling survivorships are those shown in Fig. 4.7 i.e. minor or no additional loss in *Melaleuca ericifolia, Melaleuca linariifolia* and *Casuarina glauca,* but substantial depletion in *Eucalyptus robusta* at the lower elevation planting, and in *Leptospermum juniperinum* at both elevations. These saplings will be permanently marked to permit long term assessment of growth and survivorship. The establishment information for these species will be augmented following restoration programs currently being undertaken at local sites.

It is intended to maintain a photographic record of the process of natural regeneration occurring within wet meadow at Coomonderry Swamp. It would also be of great value to record establishment and growth of individual plants and species. Survivorship and growth of species, naturally regenerating at different elevations, would make a useful comparison to the experimental data.

5.3.4 Faunal surveys

While some work on the herpetofauna generally (Murphy 1994) and on the Green and Golden Bell frog specifically (Daly 1995) has been carried out at Coomonderry Swamp, there remains much work to be done. Mammal and bird records include numerous rare, vulnerable and even extinct species, yet only superficial surveys of these groups have been performed. It would be particularly valuable to understand how the fauna utilize Coomonderry Swamp under varying conditions of inundation and, for the avifauna, in response to available water elsewhere.

5.4 Studies at other Australian wetland centres pertinent to the conservation and management of wetlands on the NSW south coast.

The recent INTECOL conference (see Department of Environment & Planning, WA 1996) indicated several programs of wetland research and protection which could be implemented, or applied to great advantage on the south coast of NSW. Obviously many of these included overseas examples (and some have been described or cited elsewhere in this thesis). However, in this Chapter I describe three Australian examples; two dealing with propagation and establishment of herbaceous wetland species and one with regional wetland mapping. The latter is discussed in relation to an excellent mapping program currently underway in the Illawarra region. The intention is to demonstrate firstly, the need for efficient communication among wetland scientists and the imperative to publish findings (Boon & Brock 1994), and secondly, the need to collate all relevant information and present it in a form easily accessible to managers and authorities.

5.4.1 Seed bank studies

Wetland seed banks have been the subject of several programs carried out by researchers from the Botany Department, University of New England, Armidale. Some of these, reviewed by Brock & Britton (1995), included studies of: (i) the influence of inundation regime on germination; (ii) longevity and dormancy properties of seeds and (iii) seasonality and seed germination. Many of the species studied are common to the freshwater wetlands of the NSW south coast and much of the information collected on establishment requirements could be applicable despite the differences in climate experienced by the two regions.

5.4.2 Propagation and establishment of wetland plants

In Chapter 4, I discussed the value of the 'Guide to emergent wetland plants of south-western Australia' prepared by Chambers *et al.* (1995). The book was based on detailed research on propagation and establishment (Chambers *et al.* 1992). It augments earlier work on management and rehabilitation (Godfrey *et al.* 1992) and provides the first ecological text, accessible to lay persons, which describes the biology, ecology and propagation of key wetland species.

Given that the biology of local wetland species is well enough understood, and that much of the required ecological and some propagation data are available in this work and elsewhere (see Section 5.4.1), it would soon be possible to prepare a similar book for species found on the coastal plain of NSW.

5.4.3 Mapping

Mapping of important wetlands for inventory purposes has been carried out along much of the NSW south coast (e.g. Bell & Edwards 1980; Moss 1983; Adam *et al.* 1985). However Councils and other authorities require more detailed maps of local wetlands, linked to all available data, so that they can better assess the impacts of planning decisions.

Recently, within the Kiama region (Fig. 1.2), remote sensing has been used to map individual waterways and catchments (Chafer & Marthick 1995). Further mapping is underway using a geographic information system (GIS) tied to a relational database with the intention of linking a range of spatial and other wetland data for the whole Illawarra region (Young *et al.* 1996). The primary objective of Young *et al.* (1996) was to collate material from a wide range of sources on Illawarra wetlands so that information was readily accessible and easily communicated. The methods are intended to be consistent with other mapping programs in NSW (Winning & King (1995) in order to allow inter-regional comparisons.

Some aspects of the detailed wetland mapping program carried out along the coastal plain of Western Australia between Perth and Bunbury by the Water Authority of Western Australia (undated maps, Semenuik 1996) would be most relevent and applicable to the program undertaken by Young *et al.* (1996). The Water Authority of Western Australia has produced a series of large scale colour maps of wetlands together with information on geomorphology, wetland type and condition, hydrology and flora and fauna. These maps would prove an excellent reference guide to managers. It is important that detailed mapping such as this, and of the type described by Young *et al.* (1996), be continued south of the Illawarra catchment.

5.5 Coomonderry Swamp as an Australian listed Ramsar site - a proposal

Throughout this thesis I have emphasised the significant ecological values of Coomonderry Swamp. By way of conclusion, I briefly address some of the criteria identifying wetlands of international importance (ANCA 1996) to Coomonderry Swamp. Wetlands need to meet at least one of these criteria to be listed by Ramsar. Contracting Parties to Ramsar have an obligation to care for all wetlands, but as the public face of Ramsar, internationally listed sites have a greater chance of being protected (ANCA 1996). In my judgement, Coomonderry Swamp meets at least five Ramsar criteria (with at least one in each category):

Category 1 ***Criteria for representative or unique wetlands***

1(d) *"it is an example of a specific type of wetland, rare or unusual in the appropriate biogeographical region"*

Coomonderry Swamp, at 670 ha, is one of the largest, single dunal wetlands in NSW listed in the 'Directory of Important Wetlands' (ANCA 1996). It is by far the largest wetland of this type within either the Sydney Basin or the South East Highlands biogeographical regions (IBRA classification - Appendix 13).

Coomonderry Swamp is a geographically isolated example of its type and has characteristics in the flora which differ from its northern counterparts. For example *Melaleuca quinquenervia* and *Lepironia articulata*, which are features of related wetlands further north, do not occur on the south coast of NSW. Coomonderry Swamp has a woody margin typified by *Eucalyptus robusta, Melaleuca ericifolia, Melaleuca linariifolia, Casuarina glauca* and *Leptospermum juniperinum.*

Category 2 *General criteria based on plants or animals*

2(a) *"it supports an appreciable assemblage of rare, vulnerable or endangered species or subspecies of plant or animal, or an appreciable number of individuals of any one or more of these species"*

Coomonderry Swamp supports the largest stands of *Eucalyptus robusta* and the rare Running Marsh Flower, *Villarsia reniformis* in the Sydney Basin biogeographic region. Stands of both species are substantial but no data were available to allow comparisons to populations elsewhere.

Rare or uncommon NSW plant species include *Lilaeopsis polyantha* and *Desmodium varians. Cyperus odoratus* had previously been recorded at only three north coast wetlands (Pressey 1987). Numerous plant species at Coomonderry Swamp are of regional importance. Some unusual hybrids of *Juncus* spp. have been recorded as well as undescribed forms of *Lilaeopsis polyantha* and *Persicaria lapathifolia.*

The Green and Golden Bell frog, *Litoria aurea,* an endangered species (Threatened Species Conservation (TSC) Act Schedule 1 1995), is, at times, common at Coomonderry Swamp (Daly 1995; de Jong pers. obs.). The Tiger Quoll, *Dasyurus maculatus,* and the Yellow-bellied glider, *Petaurus australis* are vulnerable species (TSC Act Schedule 2 1995) which have been previously sighted within adjacent forest (Kevin Mills & Associates 1993). Several vulnerable avifauna have been sighted at Coomonderry Swamp or in adjacent areas (Kevin Mills & Associates 1993). These include: the Australasian Bittern (*Botaurus poiciloptilus*), the Black Bittern (*Dupetor flavicollis*), the Black-necked Stork (*Xenorhynchus asiaticus*) and the Glossy Black

Cockatoo (*Calyptorhynchus lathami*). The fauna, however, are poorly studied.

2 (b) *"it is of special value for maintaining the genetic and ecological diversity of a region because of the quality and peculiarities of its flora and fauna"*

Coomonderry Swamp is geographically isolated, yet it is largely unspoiled, supports over 200 plant species, at least 117 bird species (but records are poor), and a diversity of plant communties. Given that almost all other freshwater wetlands in the biogeographic region are extensively degraded, Coomonderry Swamp must be considered the most valuable freshwater wetland ecological and genetic resource in the region.

In addition, because of its proximity to the substantial Crookhaven - Shoalhaven estuarine system, it represents an important drought refuge for avifauna. The potential for re-afforestation of the habitat corridor linking Coomonderry Swamp and Seven Mile Beach open-forest to extensive undisturbed vegetation of the hinterland should be noted (Kevin Mills & Associates 1993).

2 (d) *"it is of special value for one or more endemic plant or animal species or communities."*

Coomonderry Swamp and its margins harbour the most diverse range of communities at a single site anywhere on the south coast of NSW. These include: extensive sedgeland, wet meadow, floating mats, ephemeral mud, *Eucalyptus robusta - Gahnia,* and littoral rainforest communities.

Category 3 *Specific criteria based on waterfowl*

3 (b) *"it regularly supports substantial numbers of individuals from particular groups of waterfowl, indicative of wetland values, productivity or diversity."*

No comprehensive temporal studies have been carried out. However Lawler & Porter (1990) found Coomonderry Swamp supported the greatest diversity of bird habitats and bird species in their survey of Nowra district wetlands.

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Appendix 1 Wetland definitions adopted for this thesis.

In terms of legislation and conservation two wetland definitions were considered to be most relevant to this study. These were:

(i) **The NSW Wetlands Management Policy** (Department of Land & Water Conservation 1996) defines wetlands as *"land that is:*

- *inundated with water on a temporary or permanent basis;*
- *inundated with water that is usually slow moving or stationary;*
- *inundated with water that is shallow; and*
- *inundated with water that may be fresh, brackish or saline".* (The policy covers all natural wetlands).

(ii) **The Directory of Important Wetlands** (ANCA 1996) defines wetlands according to the Ramsar Convention, namely:

"areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres"

The NSW wetlands management policy definition is a subset of the very broad Ramsar definition, and all wetlands referred to in this thesis (other than one or two wetland creation sites) fall within the former definition.

Appendix 2 Wetlands and drainage of the Shoalhaven alluvial plain - historical accounts.

Three extracts are presented which indicate the previous extent of wetlands on the Shoalhaven River alluvial plain and portray historical attitudes to them.

(i) **From a description of a journey by Mr. Justice Field from Kiama to Coolangatta Settlement beginning the week of 20th October 1823:**

"21st. October: Ascended with Mr. Berry the mountain called by the natives "Coolangatta" under which he is building his house ...." (he continues):

"Although I'm afraid Mr Berry's land will hardly repay him for his outlay upon them yet whoever extends the settling of N.S.W. further and anybody else who has gone before him is a benefactor to the Colony. I fear in this case man has taken possession before Nature has done her work. Immense swamps and lagoons have only been just left by the sea and the present land is yet indifferent to grazing. Still, though the cedar grounds end before the Shoalhaven is reached, the sea is opened for any exportable produce that can be raised upon patches of alluvial soil lying on the alternative projecting points of the river".

(ii) **In a chapter on 'Public Health' Antill (1982) made a series of references to swamps e.g:**

"The early settlers in the Shoalhaven were fortunate in having as their mentor Alexander Berry, a qualified physician with a wide experience in sicknesses and diseases who put this concern into practice. Extensive drainage of swamps and backwaters secured a cleaner district and the removal of mosquitoes and flies which could transmit sickness and disease. ...." and;

"Drainage was a perpetual problem in the Nowra township, the natural run-off being towards the swampland between East Street and Worrigee Hill, known later as the East Street Swamp, and from there by seepage, more than direct run-off, into the Shoalhaven River.

Thus large areas of stagnant water were created after heavy rain in which mosquitoes and flies bred without restraint.

Successive councils considered this to be the greatest health hazard the township faced ...."

(iii) From a brief history reprinted as originally appeared in a newspaper at this time: 'The Coolangatta Estate, Shoalhaven' by Alex. Hay, *c.* 1910:

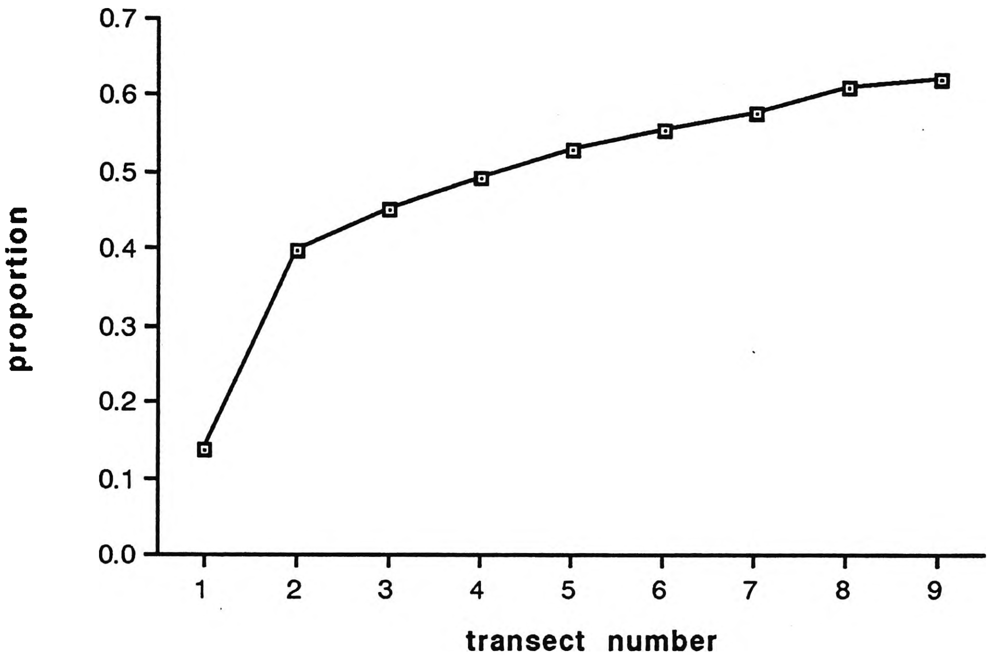
"The entire area of the Estate at this time amounted to 100 square miles. Of this area 40 square miles consisted of alluvial flat land. In its natural state this land consisted of a series of freshwater marshes with surfaces in their lowest, some 3 or 4 feet below the flood level of the district in which they lie". .... he continues:

"Another leading feature of the Marsh-reclamation Scheme is the freedom of floods when they rise above the natural banks of the River and Creek to flow freely into the reclaimed basins. There they stop for 3 or 4 days until the flood has passed to sea and the Shoalhaven resumes its normal tidal action. The imprisoned flood-water after it has dropped its fatness in the form of silt, then passes out through the sluices and flood escapes. Like the Egyptians of the Nile Valley we "welcome the coming, speed the parting guest". To the remark of Judge Barron Field uttered when viewing the dismal array of swamps from Coolangatta Hill on October, 1823, that "Man (in the shape of Berry and Wollstonecraft) had taken possession before Nature had done her work", we might reply that man now helped her accomplish her task of raising the surfaces of the flats in her own appointed way - only he bustled her into quicker action.

The system of drains, small and large, that carry on the work of water-discharge, amount, in the total, to a length of about 150 miles; of sluices that guard the reclaimed area from tidal water, there are some 25 with waterways ranging from 4 up to 150 square feet. ...."

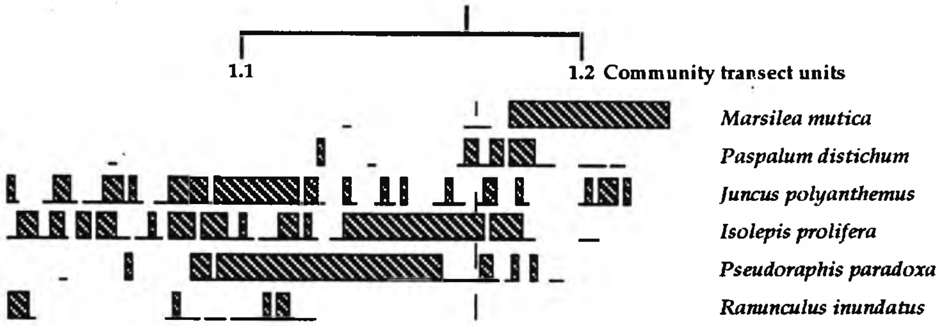
These extracts were reprinted with permission from R. G. Antill's 'Settlement in the South' (Weston & Co. Publishers Pty. Ltd., Kiama 1982)

Appendix 3 Cumulative proportion of total species (211) recorded at Coomonderry Swamp and margins following each transect survey.

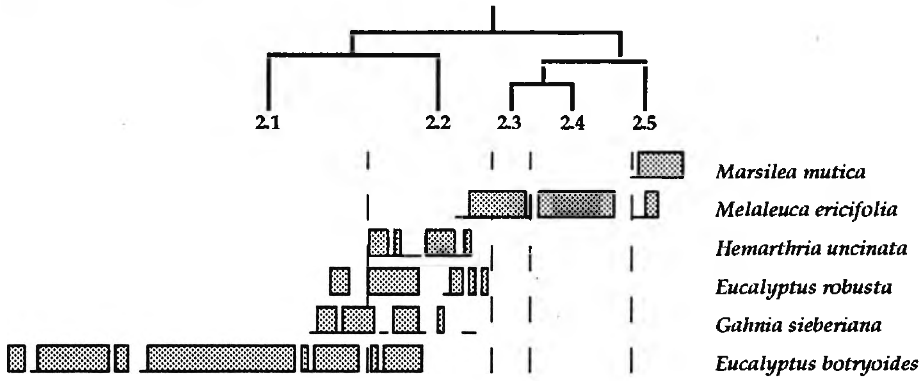


Appendix 4 Community transect divisions derived from TWINSPAN analysis of species composition in quadrats along all transects at Coomonderry Swamp (excluding Transect 3, Fig. 2.4). Direct gradient analysis shows the distribution and abundance of some key indigenous species. Lines show presence of named species. Shaded bars show % cover ≥ ten. Note: (i) that transects are started and finished in relatively homogeneous units of vegetation or open water; (ii) that 'community' divisions were defined by many more species than are shown in the DGA; (iii) a few quadrats clustered out of sequence are not shown by dotted lines (but see the order of clustering for Transect 7).

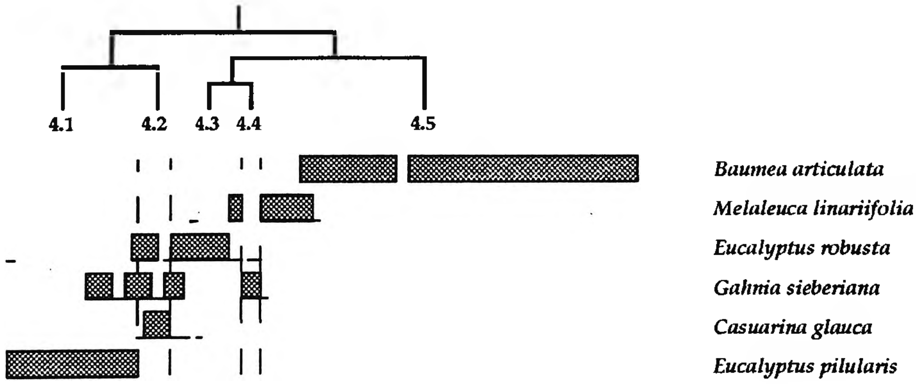
Transect 1



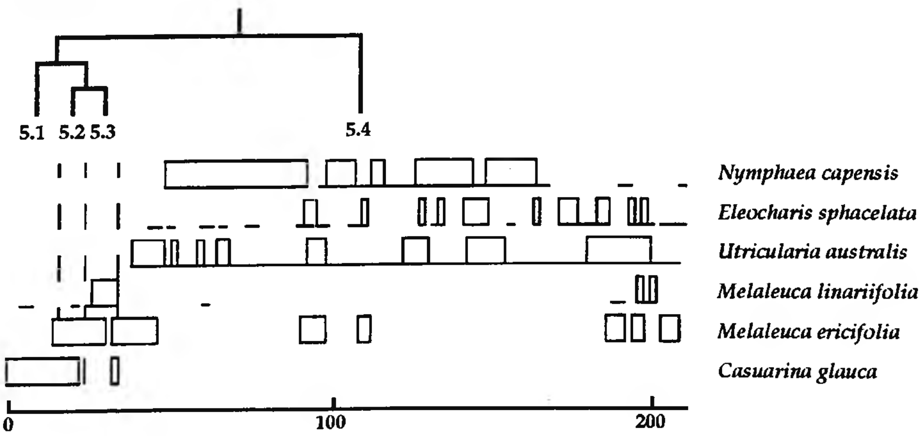
Transect 2



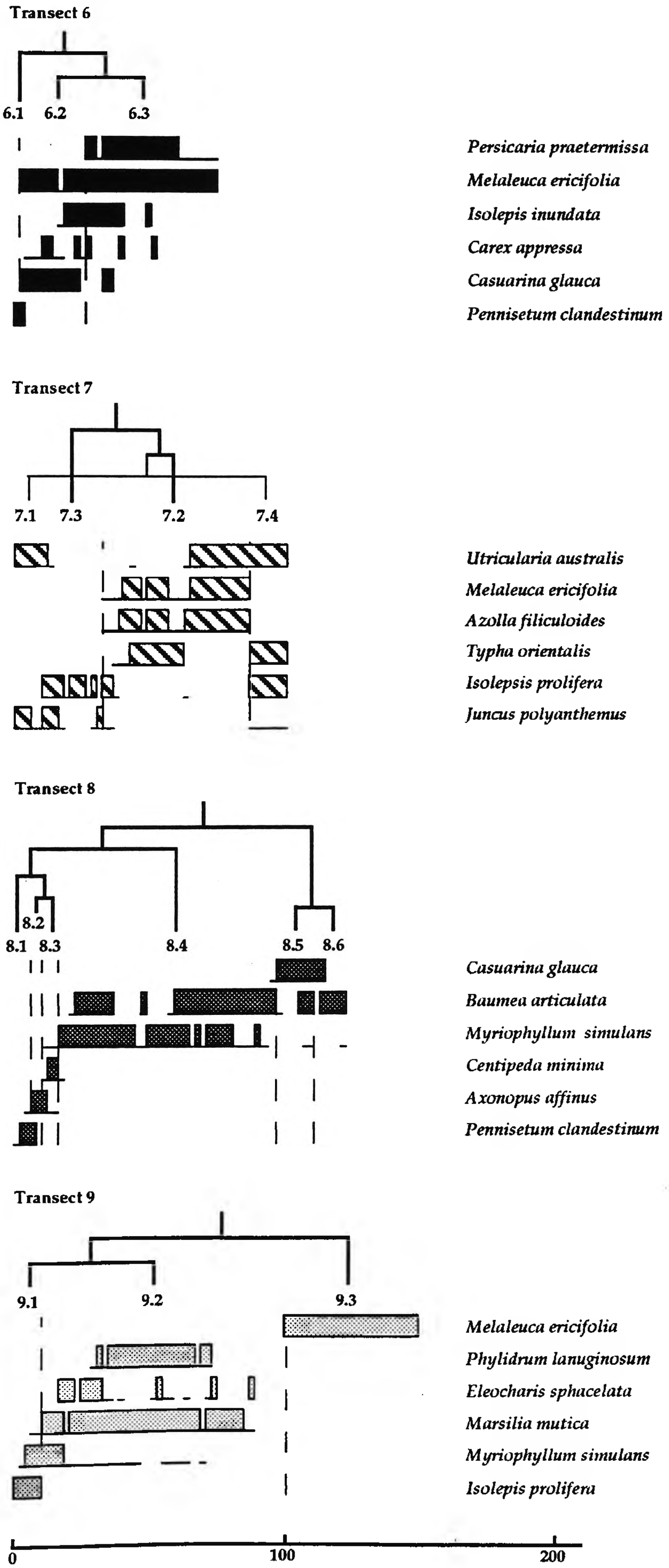
Transect 4



Transect 5



Appendix 4 (continued) Community transect divisions derived from TWINSPAN and direct gradient analysis of species (Transects 6 - 9).



Appendix 5 Vascular plant species recorded from nine wetlands (and humic soil margins) on the south coast of NSW. Nomenclature follows Harden (1990-93) and recent revisions accepted by the National Herbarium of NSW.

*	introduced taxon	•	at, or near (< 20 km), limit of known range (Harden 1990-93)
◊	protected species in NSW (Harden 1990-93)	••	beyond limit of known range (Harden 1990-93)
##	rare or uncommon species in NSW (Harden 1990-93)	Δ	new record for ecogeographic region (Harden 1990-93)
#	regionally rare, uncommon or poorly conserved species (after Benson & McDougall 1993-95 or Mills & Jakeman 1995)		
?	insufficient material for positive identification at that wetland		
	Bold type denotes abundance: ≥ 10% cover in any quadrat within a representative community		

Communities (see Fig. 2.14)

DM	dry meadow	WM	wet meadow	DF	deep freshwater	ME	*Melaleuca*	SS	Swamp mahogany - saw-sedge		
SE	sedgeland	OF	open forest	GL	grassland	SM	saltmarsh	MA	mangrove		

Wetlands (see Fig. 1.2)

K	Killalea Lagoon	We	Werri Lagoon	C	Crooked River	B	Brundee Swamp	Te	Terrara Swamp
P	Pattimores Lagoon	Ta	Tabourie Lake	Wi	Willinga Lake	Co	Coomonderry Swamp		

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
PTERIDOPHYTA										
AZOLLACEAE										
Azolla filiculoides var. *rubra*	K	Co	Co K	Co						
BLECHNACEAE										
•◊*Blechnum indicum*					Co					
B. cartilagineum							Wi			
Doodia aspera							Co			
DENNSTAEDTIACEAE										
Hypolepis muelleri		Co								
Pteridium esculentum				P Ta Wi	**Co**		**Co B P Ta Wi**			
GLEICHENIACEAE										
Gleichenia dicarpa					Co		Wi			
MARSILEACEAE										
Marsilea mutica		Co	**Co**							
SELAGINELLACEAE										
Selaginella uliginosa				Ta Wi			Ta			

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
GYMNOSPERMAE										
ZAMIACEAE										
Macrozamia communis							Co			
ANGIOSPERMAE										
- MONOCOTYLEDONS										
ALISMATACEAE										
Alisma plantago-aquatica		Co	Co							
**Sagitaria graminea* subsp. *platyphylla*	K		Co K							
ASPARAGACEAE										
**Protasparagus aethiopicus*								We		
ASPHODELACEAE										
*• •*Trachyandra divaricata*	K									
COMMELINACEAE										
Commelina cyanea				Co			Co	We	We	
CYPERACEAE										
• •*Baumea arthrophylla*			Co	Wi	Co	Co				
B. articulata			Co K	Co	Co	Co				
B. juncea				P Ta Wi	Co		Co		P	
B. rubiginosa					Co					
Bolboschoenus ?caldwellii		Te B	K							
B. fluviatilis		Co	Co							
Carex appressa		Co		Co				Co		
C. inversa	K									
**Cyperus brevifolius*		Co								
•*C. laevis*							Co			
Δ##• •*C. odoratus*		Co								
C. polystachyos	K	Co K B		Co						
C. sanguinolentus		Co								
Eleocharis acuta	K	Co K Te B	Co	B				B		

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
*• *E. minuta*		Co								
E. sphacelata		**Co**	**Co K**							
• *Fimbristylis velata*		CoK								
Gahnia sieberiana			Co	**Co P Ta Wi**	**Co**		**Co C Ta Wi**			
Isolepis cernua		Co K								
I. fluitans		Co B	**Co**	Co	Co	Co				
I. inundata		Co B		**Co Wi**						
I. nodosa	**K**						Ta			
Δ#*I. platycarpa*									**We**	
**I. prolifera*	**K**	**Co B**	**Co**	**Co**						
Lepidosperma laterale							Wi			
Schoenoplectus validus		Co B Te	**Co K**							
Schoenus brevifolius				**Ta** Wi	Co		**Ta**			
S. maschalinus		Co			Co					
S. nitens				Wi						
HYDROCHARITACEAE										
Ottelia ovalifolia			Co							
Vallisneria gigantea			K							
JUNCACEAE										
Juncus continuus		Co		B Wi	Co					
##*J. continuus* X *usitatus*							Co			
**J. cognatus*		Co						Co		
J. kraussii subsp. *australiensis*				**B P Ta Wi**			C	**We**	**We C B P**	
J. mollis				**B**					**B**	
J. planifolius		Co	Co	Wi						
••Δ*J. polyanthemus*		**Co Te B**	**Co**	B ?Wi					B	
J. polyanthemus X *usitatus*		Co								
##*J. polyanthemus* X *procerus*		Co	Co							

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
J. prismatocarpus		Co K	Co	Co	Co					
J. procerus		Co	Co	Co						
#J. subsecundus			Co							
J. usitatus		Co						Co		
JUNCAGINACEAE										
Triglochin procerum s. lat.		Co B	Co K	Co						
T. striatum	K	Co K Te B			Co				We B P	
LEMNACEAE										
•*Lemna ?disperma*			Co							
Spirodela punctata	K		Co K	Co						
LOMANDRACEAE										
Lomandra ?confertifolia subsp. *rubiginosa*							Wi			
L. longifolia				Wi			Co C B Ta Wi			
?Lomandra sp.							C			
LUZURIAGACEAE										
Eustrephus latifolius							Co Ta			
Geitonoplesium cymosum							Co C			
ORCHIDACEAE										
Acianthus ?fornicatus							Co			
Caladenia carnea var. *carnea*							Co			
Cryptostylis subulata					Co					
Dipodium ?punctatum							Co			
Spiranthes sinensis subsp. *australis*		Co		Wi						
PHILYDRACEAE										
Philydrum lanuginosum		Co B	Co	Co						
PHORMIACEAE										
Dianella caerulea var. *caerulea*					Co		Co Wi			

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
POACEAE										
Agrostis avenacea var. *avenacea*	K	Co K							B	
**Andropogon virginicus*		Co					Co			
**Axonopus affinus*		Co		Co	Co			Co		
**Bromus cartharticus*		Co						We		
Cynodon dactylon	K	Co		Co				We	We C	
Deyeuxia quadriseta				Ta Wi						
Dichelachne inaequiglumis							Co			
**Digitaria ciliaris*		Co								
**Echinochloa crus-galli*		Co Te						We		
Echinipogon caespitosus var. *caespitosus*				Ta			Co C			
Entolasia marginata				Co	Co		Co C Wi			
E. stricta				B Ta Wi	Co		Co C Ta Wi			
**Eragrostis mexicana*							Co			
Hemarthria uncinata				Ta Wi	Co					
**Holcus lanatus*	K	Co								
Imperata cylindrica var. *major*				B Ta Wi			Co C B Ta Wi			
**Lolium ?multiflorum* and hybrids		Co								
**L. perenne*	K									
Microlaena stipoides var. *stipoides*							Co			
Oplismenus aemulus				Co P Ta	Co		Co			
Panicum simile		Co					B			
**Paspalum dilatatum*		Co								
P. distichum		Co K Te B	Co	Co	Co					
* • *P. urvillei*		Co								
P. ?vaginatum	K								We	
**Pennisetum clandestinum*	K	Co Te		Co				Co We	We C	

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
*Phalaris angusta		Co								
*P. aquatica		Co ?K								
Phragmites australis				P Ta Wi	Co			We	We C B P	
*Polypogon monspeliensis		Co							We	
Pseudoraphis paradoxa		Co	Co	Co	Co					
Sacciolepis indica		Co								
*Setaria gracilis								We		
*S. pumila								Co		
Spinifex sericeus	K Ta									
*Sporobolus indicus var. capensis	K									
S. virginicus var. virginicus				Ta					C	C
*Stenotaphrum secundatum							C	We	We C	
Themeda australis							Co			
Zoysia macrantha	K		K							
POTAMOGETONACEAE										
Potamogeton ochreatus			Co							
P. tricarinatus			Co							
Potomageton sp.				Co						
RESTIONACEAE										
◊••Restio tetraphyllus subsp. meiostachyus				Wi			Co			
SMILACACEAE										
Smilax glyciphylla					Co		Co			
SPARGANIACEAE										
Sparganium subglobosum		Co								
TYPHACEAE										
Typha orientalis	K	Co K B	Co K Te							
ZOSTERACEAE										
Zostera capricorni: deep estuarine at WE C Ta										

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
ANGIOSPERMAE										
- DICOTYLEDONS										
AIZOACEAE										
Tetragonia tetragonoides								We	We C B	
AMARANTHACEAE										
Alternanthera denticulata	K	Co K		Co						
APIACEAE										
Apium prostratum var. *filiforme*									We	
Centella asiatica		Co		P						
**Hydrocotyle bonariensis*	K	Co K	K	Co						
H. peduncularis		Co								
##*Lilaeopsis polyantha*		K							We	
L. polyantha large phyllode form		Co								
APOCYNACEAE										
Parsonia straminea		Co		Co	Co		Co	We	C	
ASCLEPIADACEAE										
**Araujia sericiflora*								We		
Marsdenia rostrata							Co			
Tylophora barbata							C			
ASPARAGACEAE										
**Protasparagus aethiopicus*								We		
ASPHODELACEAE										
*••*Trachyandra divaricata*	K									
ASTERACEAE										
**Aster subulatus*	K	Co K Te B						We	We B	
**Bidens pilosa*								We		
**Bidens tripartita*		Co								
Centipeda minima var. *minima*		Co	Co	Co						

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
**Chrysanthemoides monilifera* subsp. *rotundata*							We			
**Conyza albida*	K	Co		Ta			C			
**Conyza parva*		Co								
**Cotula coronopifolia*	K	Co **B**	**K**	B					**We B**	
Euchiton involucratum		Co								
**Facelis retusa*		Co								
**Hypochaeris glabra*		Co		Wi				**We**	**We**	
**H. radicata*	K	Co K Te							We	
Lagenifera gracilis							Co			
#*Leptinella longipes*				Wi				**We**	**We**	
**Onopordum acanthium* subsp. *acanthium*		Co Te						We		
Ozothamnus diosmifolius				P			Co Wi			
Pseudognaphalium luteoalbum		Co K								
**Senecio madagascariensis*	K	Co K Te	Co					We	We	
**Sonchus asper* subsp. *glaucescens*		Co								
**S. oleraceus*		Co K	K							
Vernonia cineria var. *cineria*							Ta			
*• •*Xanthium occidentale*		Te								
AVICENNIACEAE										
Avicennia marina var. *australasica*									C	C
BRASSICACEAE										
#*Cardamine paucijuga*		Co								
*##*Lepidium bonariense*								We		
CALLITRICHACEAE										
**Callitriche ?stagnalis*		Co								
CARYOPHYLLACEAE										
**Silene nocturna*	K									
*• •*Spergularia marina*									We B	

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
CASUARINACEAE										
Allocasuarina littoralis							Co			
Casuarina glauca	K	Co B	Co	Co B P Ta Wi	Co	Co	C	We	We C	
CHENOPODIACEAE										
**Atriplex prostrata*									We C	
Chenopodium glaucum		K								
Suaeda australis									C	C
Sarcocornia quinqueflora subsp. *quinqueflora*								We	We C P	C
CLUSIACEAE										
Hypericum gramineum					Co					
CONVOLVULACEAE										
Dichondra repens							Co C		C	
#*Polymeria calycina*					Co					
CRASSULACEAE										
#*Crassula peduncularis*		K								
C. seiberiana	K									
DILLENIACEAE										
Hibbertia diffusa							B			
H. ?obtusifolia							Wi			
#*H. scandens*	K			Co P Ta			Co C Ta Wi			
DROSERACEAE										
Drosera spatulata				Wi	Co					
ELAEOCARPACEAE										
Elaeocarpus reticulatus					Co		Co Wi			
ELATINACEAE										
#*Elatine gratioloides*		Co		Co	Co					
EPACRIDACEAE										
Leucopogon lanceolatus var. *lanceolatus*							Co Wi			

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
Monotoca elliptica							Co Ta			
ESCALLONIACEAE										
Polyosma cunninghamii							C			
EUPHORBIACEAE										
Breynia oblongifolia				P			Co C Ta Wi			
##*Chamaesyce sparrmanii*	K									
#*Glochidion ferdinandi* var. *ferdinandi*					Co		Co			
Poranthera microphylla							Co			
FABACEAE - FABOIDEAE										
Daviesia ulicifolia							B			
Desmodium brachypodum							Co			
•*D. rhytidophyllum*							Co			
D. varians				Ta			Co C			
Glycine clandestina species complex				Ta Wi			Co C B Wi			
Hardenbergia violacea							Wi			
Kennedia rubicunda				B Wi			Co C B Ta Wi			
Pultenaea daphnoides							Wi			
P. retusa				B Wi			B			
**Trifolium repens*	K	Co B						Co		
FABACEAE - MIMOSOIDEAE										
Acacia falcata							B			
A. implexa							Co P			
A. longifolia	K			B P Ta Wi	Co		Co ?C B Ta Wi			
A. mearnsii							Co			
A. suaveolens							Co			
A. ulicifolia							Co			

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
FUMARIACEAE										
**Fumaria* sp.		Co								
GOODENIACEAE										
•*Goodenia heterophylla* subsp. *eglandulosa*							Co			
G. ovata				P Wi			Wi			
G. paniculata		Co		B Wi	Co					
Selliera radicans				P Wi				We	We B P	
HALORAGACEAE										
Gonocarpus micranthus subsp. *micranthus*					Co					
G. teucrioides							Co Ta Wi			
?*Haloragis heterophylla*							Wi			
*•*Myriophyllum ?aquaticum*		B								
•*M. simulans*	?K	Co ?K ?B	Co	Co	Co					
•*M. verrucosum*		K								
HYDROCHARITACEAE										
Vallisneria gigantea			K							
LAMIACEAE										
*•*Plectranthus ?ciliatus*								We		
LAURACEAE										
Cassytha pubescens				B P Ta Wi			C Ta			
*•*Cinnamomum camphora*				Co						
LENTIBULARIACEAE										
Utricularia australis			Co	Co	Co					
U. dichotoma					Co					
LOBELIACEAE										
Lobelia alata		Co		Co	Co					
Pratia purpurascens				B P			Wi			

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
LYTHRACEAE										
Lythrum hyssopifolia		Co							B	
MALVACEAE										
**Sida rhombifolia*				Co						
MENISPERMACEAE										
Stephania japonica var. *discolor*							Co C			
MENYANTHACEAE										
Villarsia exaltata		Co	Co	Co	Co	Co				
V. reniformis		Co	Co	Co	Co	Co				
MYOPORACEAE										
Myoporum acuminatum							Co			
M. boninense subsp. *australe*							Co C			
MYRTACEAE										
Angophora floribunda							Co			
Callistemon citrinus					Co					
Eucalyptus botryoides				P Ta Wi	Co		Co C Ta Wi			
E. botryoides X saligna							Co			
•*E. ?imitans*							B			
E. pilularis				B			Co B Wi			
#*E. robusta*				Co B ?Wi	Co	Co	Co			
#*Leptospermum juniperinum*		Co		Wi	Co	Co	Co Ta			
L. laevigatum	Ta									
L. polygalifolium subsp. *polygalifolium*				Wi						
Melaleuca ericifolia		Co B	Co	Co B P Ta Wi	Co		C Wi		C	
•*M. linariifolia*			Co	Co	Co		Co Wi			
•Δ*M. styphelioides*				Co B						
Syzigium australe							C			

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
NYMPHAEACEAE										
*Δ*Nymphaea alba* and hybrids		Co	Co	Co						
*•*N. capensis*			Co							
?•*Nymphoides geminata*				Co						
OLEACEAE										
Notelaea venosa							C Ta Wi			
ONAGRACEAE										
Ludwigia peploides subsp. *montevidensis*	K	Co	Co K	Co						
OXALIDACEAE										
*•*Oxalis corniculata*		Co								
O. perennans	K									
PASSIFLORACEAE										
#*Passiflora herbertiana* subsp. *herbertiana*							Co			
PHYTOLACCACEAE										
**Phytolacca octandra*				B						
PITTOSPORACEAE										
Billardiera scandens var. *scandens*				P			Co Ta Wi			
B. scandens var. *scandens/sericata* intergrade							Co B			
Pittosporum revolutum							Co C			
P. undulatum							Co C P			
PLANTAGINACEAE										
**Plantago lanceolata*	K									
POLYGONACEAE										
**Acetosella vulgaris*		Co								
Persicaria decipiens	K	Co B	Co	Co						
P. hydropiper		Co								
P. lapathifolia		Co Te								
P. lapathifolia (form with hairy underleaf)		Co								
P. orientalis		Co								

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
P. praetermissa		Co	Co	Co B				We		
**Polygonum aviculare*		Te							Te	
**Rumex crispus*		Co								
PRIMULACEAE										
**Anagallis arvensis*	K									
Samolus repens				Ta Wi					We C	
PROTEACEAE										
Banksia integrifolia subsp. *integrifolia*					Co		Co Ta	We		
B. serrata							Co Ta			
B. spinulosa var. *spinulosa*							Wi			
Persoonia linearis							Co ?B			
RANUNCULACEAE										
Clematis aristata							Co Wi			
Ranunculus inundatus	K	Co K B	K	B						
R. ?lappaceus				B						
ROSACEAE										
**Rubus* complex		Co						Co		
Rubus parvifolius							Co C			
RUBIACEAE										
Galium propinquum				Ta						
Opercularia aspera							Wi			
O. ?varia							Co B			
RUTACEAE										
##•*Melicope micrococca*							Co			
Zieria smithii subsp. A							Co			
SALICACEAE										
**Salix alba*		Co								
SANTALACEAE										
Choretrum candollei				Wi						
Exocarpus cupressiformis					Co		Co			

	DM	WM	DF	ME	SS	SE	OF	GL	SM	MA
SCROPHULARIACEAE										
• •*Bacopa monnieri*		K							We	
Gratiola pedunculata		Co								
Mimulus repens		K							We	
Veronica plebeia							Co			
SOLANACEAE										
**Lycium ferocissimum*								We		
Solanum americanum		Co								
**S. nigrum*								We		
**S. pseudocapsicum*									C	
STACKHOUSIACEAE										
Stackhousia viminea					Co					
STYLIDIACEAE										
Stylidium graminifolium							Co			
THYMELAEACEAE										
Pimelia linifolia subsp. *caesia*							B Wi			
Pimelia linifolia subsp. *linifolia*							Wi			
VERBENACEAE										
**Lantana camara*	K						Co C			
VIOLACEAE										
Viola caleyana		Co								
V. hederacea		Co		Co B Wi	Co		Co B Wi			
VITACEAE										
#*Cayratia clematidea*							Co			
Cissus hypoglauca							Co			

Appendix 6 Two-way table derived from Bray-Curtis measure with UPGMA fusion procedure for vascular plant species recorded from nine wetlands (and humic soil margins) on the south coast of NSW.

Full names of communities and species given in Appendix 5 (only species on transects shown here). Community abbreviations are read vertically (see Fig. 2.14). Species affinities are indicated in the far right hand column. Numbers indicate distribution of species within each community transect unit: '1' least to '5' greatest (based on the % frequency occurrence of species in quadrats).

```
                    DM    WM           DF           OF     SS    SE         ME             SM      GL    MADE
                    KKK|88K1977TB|KKKKKKK7451298K|CBTW423|243843|38|B9B4B2265PTWPTWB7556|WWWPBCCC|WWWW86|CCC|WCT
                    132|..3....e1|1223311.......1|22ai...|......|..|1.1.2....1ai1ai1....|eee12121|eeee..|122|e2a
                    aaa|23b11241a|bcbdcce3542524d|aa11111|233622|45|b3d4b3433a11b11c1122|123ccabc|132311|bcd|1e1
                       |       a |               |  aa   |      |  |          bb cc     |aba     |bcab  |   |c d
                       |         |               |       |      |  |                    |        |      |   |
P. hydropiper          | 2 2     |               |       |      |  |                    |        |      |   |     WM
J. procerus            | 2 2     |          1    |       |      |  |        2           |        |      |   |
J. planifolius         | 2       |             1 |       |      |  |           1        |        |      |   |
P. luteoalbum          | 41 2    |               |       |      |  |                    |        |      |   |
H. peduncularis        |5  32    |               |       |      |  |                    |        |      |   |
P. dilatatum           |32  3    |               |       |      |  |                    |        |      |   |
S. indica              |3        |               |       |      |  |                    |        |      |   |
C. brevifolius         |32       |               |       |      |  |                    |        |      |   |
A. affinus             |55       |               |       |2     |  |              1     |        |    2 |   |
T. repens            1 |34       |               |       |      |  |                    |        |    2 |   |
C. dactylon         45 |52       |               |       |      |  |                 5  |1     1 |1     |   |
H. radicata         2 3|  213  1 |               |       |      |  |                   2|  1   1 |    2 |   |
Rubus complex          |         |               |       |      |  |                    |        |    2 |   |
S. rhombifolia      1  | 2       |               |       |      |  |                 1  |      1 |    2 |   |
-----------------------+---------+---------------+-------+------+--+--------------------+--------+------+---+---
I. prolifera        31 |  55555 2|    2  2  2  1 |       |      |  |       2          42|        |      |   |     WM
P. decipiens        12 |3 324 5 3|  225  1    1  |       |      |  |                  41|        |      |   |      +
B. tripartita          |   2355  |       1       |       |      |  |      2             |        |      |   |     DF
T. procerum            |   1455 1|       121 231 |       |      |  |       1            |        |      |   |
J. polyanthemus        |35 433542|       1  3 1  |       |      |  |2              45   |        |      |   |
M. simulans         1  | 5 142   |4         1 35 |       | 3 2  |  |     2              |        |      |   |
J. prismatocarpus      | 422325  |        1   11 |       | 42   |  |     5              |        |      |   |
P. paradoxa            |   43    |          2 21 |       |2     |  |     51            2|        |      |   |
M. mutica              |   13    |          5543 |       |      |  |                    |        |      |   |
P. distichum           |  11 4 23|       1  3    |       |      |1 |                3   |        |      |   |
P. tricarinatus        |     4   |       2 1  24 |       |      |  |                    |        |      |   |
F. velata              |    2    |               |       |      |  |                    |        |      |   |
H. glabra              |    3    |               |       |      |  |                    |        |      |   |
```

	DM	WM	DF	OF	SS	SE	ME	SM	GL	MADE	
M. ericifolia		25 2	322 3	2 1	12		5555555455554525155	1			ME
V. hederacea		5		2 2 2	1 2		12 2 1 145554				
P. praetermissa		25	111 2 1				4355 42 4		1		
C. glauca	3	5 2	1	1	22155	2	1 4 12 132 211 555	211 32	355		
C. appressa							1 1 134		4		
I. inundata		1					2 2 5 43				
C. cyanea				2 2			2	1 21	1 2		
P. straminea				1 12	3		3 122	21	2		
C. camphora							2				
E. sphacelata		1 3	554431232								DF + SS + SE
U. australis			555 4		2		1				
N. capensis			3				1				
E. gratioloides			2				1 1				
P. lanuginosum		1 1	1 31				2				
N. alba			1 11				32				
I. fluitans		12 1	1 2		1	3	3 2				
M. linariifolia			121		2		5 22				
V. reniformis			1 3		2	35	2				
B. arthrophylla			1			53	2				
B. articulata	1		2 5 5251 1 4		2243	55	21				
L. peploides	1 1	222	55 2 1				12				DF
A. filiculoides	1		555 55 3				43				
S. punctata	1		5 5 1				224				
S. validus		2	55 1								
S. graminea	1		4 4								
Chara sp.			52 5								
R. inundatus	211	12 2	2				1				DM (ecotone) + WM + SM
A. avenacea	4	23						2			
E. acuta	111	112 44	2 1				1	3			
A. subulatus	1	4 52						2 4	2 11		
C. coronopifolia		3					2 3	3 2			
B. ?caldwellii		3					2				
S. quinqueflora								35 1	1 1	235	
T. striatum	11	2 12	4					353			
S. radicans							1 2	2 134	1		

	DM	WM	DF	OF	SS	SE	ME	SM	GL	MA	DE	
L. polyantha								2				ME
B. juncea							34545	3				+
P. australis							1144	5533 21	1 2			SM
S. repens							31	442 1				
P. ?vaginatum								2				
J. kraussii				1			1 131	5 433445	2 13			SM
S. virginicus							2	552		212		+
S. australis								4		3		MA
A. marina								1		551		
S. indicus	1											DM
Z. capricorni											555	DE
M. styphelioides							4					
V. cineria				1								
O. ?varia							1					
L. bonariense									1			GL
S. secundatum				1				2 2 11	5525			+
L. longipes							1	513	3521			SM
T. tetragonoides								1 1	253			
P. clandestinum	312	3		2			1	1 1 1	354255			
S. oleraceus		3	2									WM
B. monniera		4						1				
C. peduncularis		5										
I. cernua		2										
S. alba		1										
S. nigrum							2		1			ME
R. ?lappaceus							5					(introduced)
P. octandra							5					
E. botryoides				5 54 44	1		342					OF
P. esculentum				555544	3		2311					(humic)
O. aemulus				212	3		23 3 2					+
E. stricta				2 22311	2 5		2 544111					UF
G. sieberiana			1	32313	42555		5 221 21					+
C. asiatica				1			25 11					ME

	DM	WM	DF	OF	SS	SE	ME	SM	GL	MADE	
S. brevifolius				2			3 11				
E. caespitosus				1			2				
G. propinquum							2				
D. caerulea				1 22	3 1 5						
E. cupressiformis				2	5						
B. integrifolia				2 413	1 5						
E. robusta				11	452 4	1	422				
H. uncinata					452		4				
L. juniperinum				1 1	123 35	1	3 1				
V. exaltata			1 1		353235	34	2				
G. paniculata					22 13		1 1				
L. alata					1 2		3 1				
P. calycina					2						
P. linearis				2							
D. rhytidophyllum				2							
M. communis				1							
L. gracilis				1							
S. sinensis							1				
D. spatulata							1				
J. continuus							1				
C. candellei							1 1				
L. polygalifolium							5 1				
S. uliginosa							3 1				
D. quadriseta							11				
S. asper		1									WE
P. aquatica		1									(mostly
B. fluviatilis		1	1								(introduced)
P. lapathifolia		3									
P. aviculare		1									
E. cruss-galli		1 4									
X. occidentale		1									
B. cartharticus		1						1			SM
A. prostratum								2			
I. platycarpa								3			
M. repens								3			
A. prostrata								2			
O. diosmifolius							2				OF
P. purpurascens				1			1 3				+
C. pubescens				1			2 221				ME

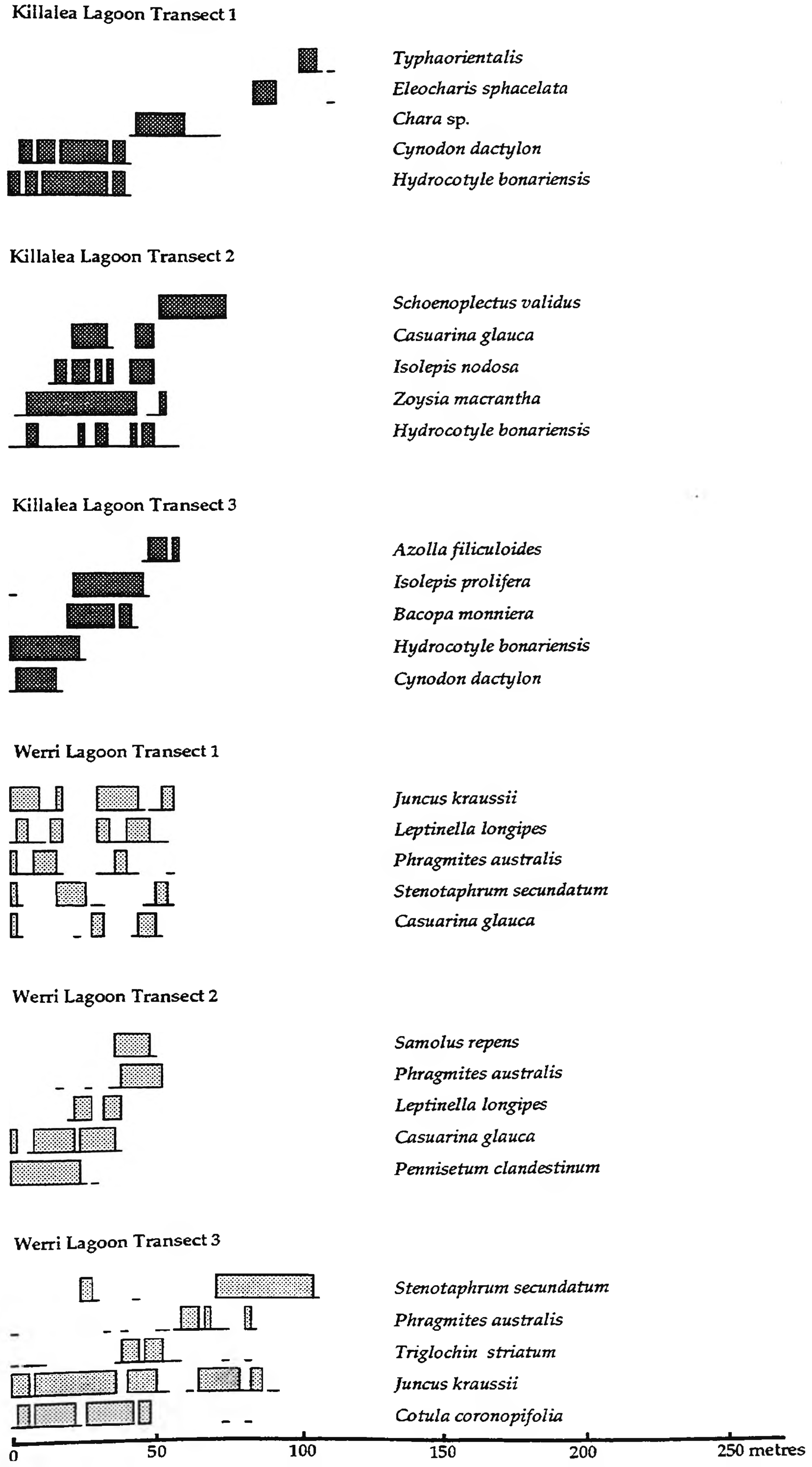
	DM	WM	DF	OF	SS	SE	ME	SM	GL	MADE		
C. parva		1315										DM
C. albida	1	1 15		1			2					+
S. americanum		5										WM
H. muelleri		5					2					
A. denticulata		5					1 1					
C. polystachyos	1	3 3 5					1					
S. madagascariensis	1 2	421 151	1				1	1 1	4312			
C. minima		5 5	1				11					
H. bonariensis	555	52 5	1 1				1 2 3					
T. orientalis	2	2 5	53 1 5									
C. sparrmanii	1											DM
A. arvensis	1											(dunal)
P. lanceolata	1 2											
S. nocturna	1											
L. perenne	1											
S. sericeus	2											
I. nodosa	133			1								
Z. macrantha	5											
T. divaricata	3											
O. perennans	2											
C. sieberiana	2											
C. inversa	1 3											
E. marginata		3		5 2 31	3		2 522					OF
B. oblongifolia				3 11 2			2					(Crooked R.)
H. scandens	1			3 2231			22 2					
D. varians				3 21			2					
L. longifolia				2322132			1					
G. clandestina				22 211			31 1					
R. parvifolius				3 1								
T. barbata				3								
G. cymosum				3 11								
P. revolutum				3 1								
Lomandra sp.				4								
S. australe				4								
N. venosa				3 11								
S. japonica				2								
L. camara	1			4 3								
M. boninense				2 21								
D. repens				2				1				

	DM	WM	DF	OF	SS	SE	ME	SM	GL	MADE	
P. cunninghamii				1							
M. elliptica				133							OF
S. glyciphylla				142	1						(Coom. 2.1)
G. ferdinandi				33	1						
E. reticulatus				3 33	2						
E. latifolius				1 12							
A. implexa				22							
P. undulatum				2 12							
B. serrata				21							
M. rostrata				2							
T. australis				1							
L. lanceolatus				1							
R. tetraphyllus				1			1				
D. brachypodum				1							
A. ulicifolia				1							
M. acuminatum				1							OF
D. ?punctatum				1							(Coom. 3.1)
Z. smithii				1							
G. heterophylla				1							
G. teucriodes				1312							OF
B. cartiligineum				3							(Willinga L.)
H. violacea				2							
L. ?confertifolia				2							
G. ovata				2			2 1				
C. aristata				1 1							
B. spinulosa				1							
O. aspera				1							
?H. heterophylla				1							
L. laterale				1							
H. obtusifolia				1			1				
I. cylindrica				41432			2 43				OF
E. pilularis				4 15			1				(lateritic)
A. longifolia				1513 11	2		2 2212				(Brundee)
K. rubicunda				142211			2 1				
B. scandens				31 21			2				
P. simile		22		4							
D. ulicifolia				5							
P. retusa				3			1 1				

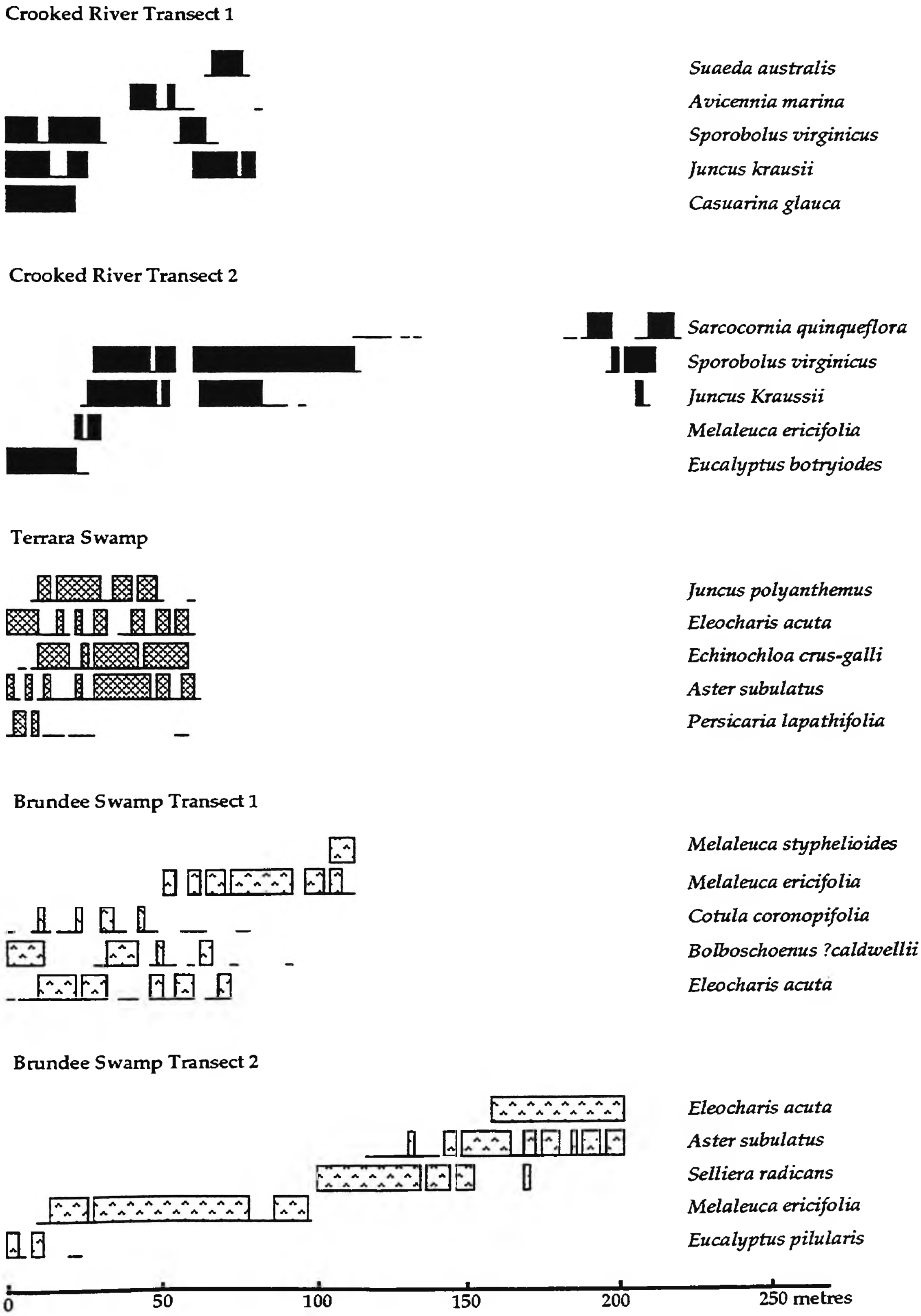
	DM	WM	DF	OF	SS	SE
E. ?imitans				3		
H. diffusa				3		
A. falcata				3		
P. linifolia				3		
O. acanthium		1 1				
S. gracilis						
P. ?ciliatus						
B. pilosa						
C. monilifera						
P. aethiopicus						
L. ferocissimum						
A. sericiflora						

ME	SM	GL	MADE	
1				
		1		GL
		1		(estuarine)
		1		(introduced)
		1		
		1		
		1		
		1		
		1		

Appendix 7 Direct gradient analysis of dominant plant species along transects at eight south coast wetlands. Lines indicate presence of named species. Shaded areas show % cover ≥ ten. (See notes App. 4.). ...cont'd



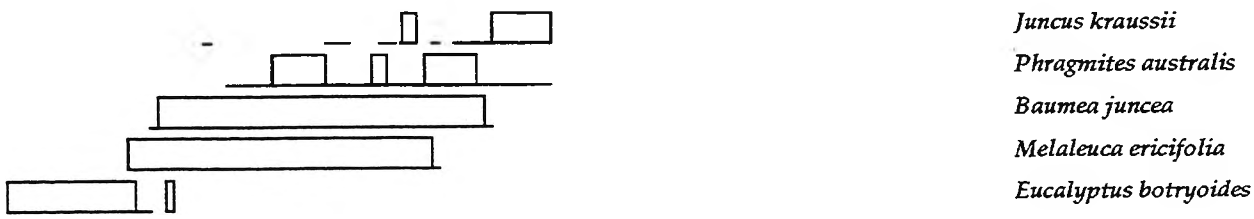
Appendix 7 (continued) Direct gradient analysis of dominant plant species along transects at eight south coast wetlands. Lines indicate presence of named species. Shaded areas show % cover ≥ ten.



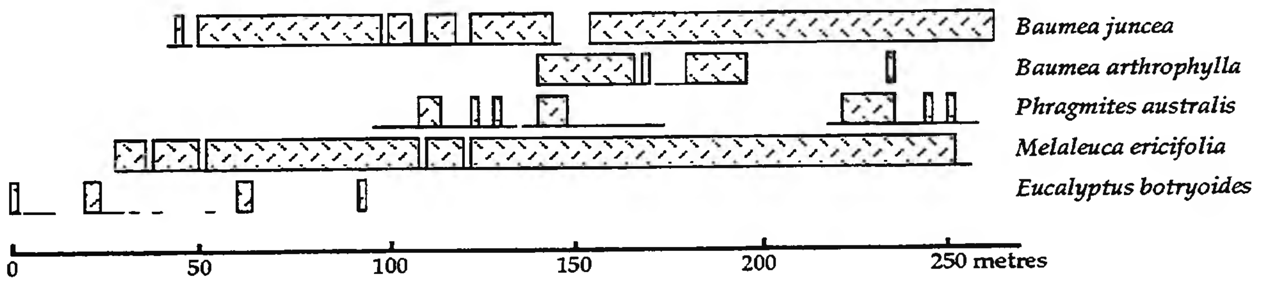
Appendix 7 (continued) Direct gradient analysis of dominant plant species along transects at eight south coast wetlands. Lines indicate presence of named species. Shaded areas show % cover ≥ ten.

Pattimores Lagoon

Lake Tabourie



Willinga Lake



Appendix 8 Two-way table for plant species recorded from community samples collected on 16 occasions over 3 years from Transect 1, along the wet meadow transition, Coomonderry Swamp.

Temporal samples of communities are read vertically i.e. '0193.1' is the first community on the transect, down the elevation gradient, and was sampled in January 1993. Full names of species are given in Appendix 5. Refer to Section 3.3.3.2 (ii) for descriptions of each group.

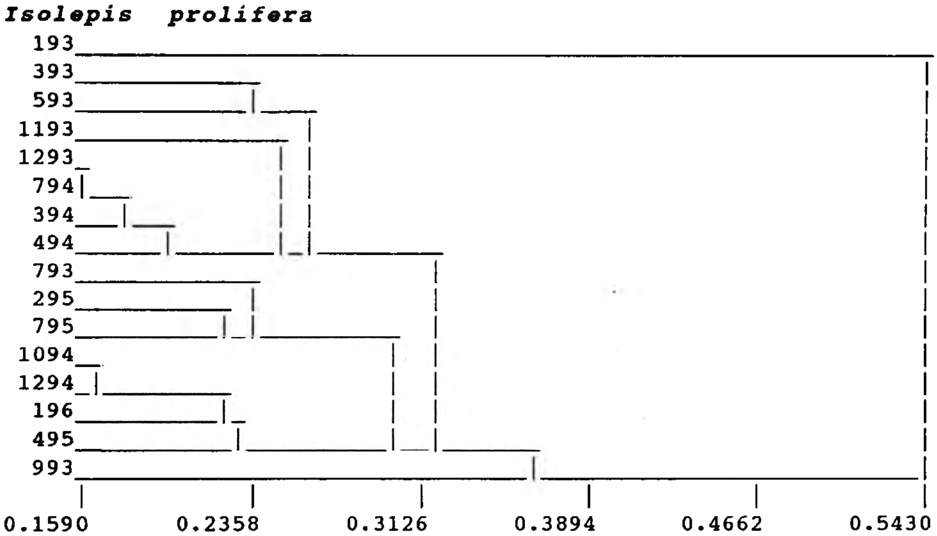
```
                  Group:           1        |  2  |     3      |4|5 |6

                           00000110001000011|00011|000100100000|0|00|11
                           13579123472247100|11310|597243272477|4|34|22
                           99999999999999999|99999|999999999999|9|99|99
                           33333334444555644|36334|334344435553|5|44|44
                           .................|.....|............|.|..|..
                           11111111111111112|22223|222222232222|3|33|34
                                            |     |            | |  |
P. hydropiper           01 331  12221111 1  |     |  1     22  | |32|
L. peploides            12 211   222212111 1|13   |  1     212 | |23|
E. cruss-galli          28 2211  1111 11    |1 1  |        2 14| |41|
B. tripartita           06 34   223  222 112|3 2  |     11 21  | |2 |
A. subulatus            54 33211 111 11211  |  1  |            | |  |
E. sphacelata           03 1111111111111  11|1 1 1| 1 1        | |  |
E. acuta                25 11111111111111112|1    | 1 11   1   | |  |
J. prismatocarpus       30 11 11 2111211121 |     |            | |  |
P. decipiens            05 333222222222112  | 2111| 1  111 1222| |  |
J. procerus             22 22222222222222222|11211|1111121 1 1 | |  |
T. procerum             18 11111111122112212|12 11|        111 | |  |
M. simulans             23 1221 1122221212 2| 1 11|   111  1   | |  |
I. prolifera            02 55554554554444445|22 21|222221212 32|2|  |
J. polyanthemus         11 44344444444444443|32222|223222212233| |  |
P. paradoxa             36 33322344434443414|33221|1  21   21  | |  |
R. inundatus            04 2222322223322324 |     |        1   | |  |
A. avenacea             08 11122332223223341|     |            | |  |
H. peduncularis         07 2321233333333325 |     |            | |  |
P. praetermissa         50        2222322321|     |            | |  |
                           -----------------+-----+------------+-+--+--
L. hyssopifolia         10 11        1      |     |            | |  |
A. plantago-aquatica    33  1               |1    |        1   | |  |
P. ochreatus            34                  |1  1 |            | |  |
C. coronopifolia        56                  |   1 | 1          | |  |
                           -----------------+-----+------------+-+--+--
B. articulata           41                  |     |          2 | |  |
                           -----------------+-----+------------+-+--+--
S. graminea             57                  |     |         1  | |  |55
                           -----------------+-----+------------+-+--+--
P. distichum            15 2 1  1121 1 1   1|12222|22133431343 | |3 |
M. mutica               27 1221111111  211 2|54555|555555555555|4|33|5
A. filiculoides         31        1    1 2 1|55332|112   231   |2|21|
S. punctata             46        1         | 4323|1           | |2 |
U. australis            32      1           |2 143|  1 31      | |22|
B. fluviatilis          17  1 1  11  111    |     |11 1    1   |2|  |
E. gratioloides         35        1         |1  13|        211 |4|23|
P. lanuginosum          37                  |121  |11      1  2|4|  |
P. lapathifolia         26 12     11 1 1    |     |      1 1   | |55|
F. velata               40        1         |     |        1   | |4 |
A. denticulata          52        1         |     |            | |2 |
                           -----------------+-----+------------+-+--+--
```

Group:		1	2	3	4	5	6
C. albida	09	11111111 111		1			
S. madagascariensis	21	11111111111 1 1					
H. radicata	14	1 111111 1111					
I. fluitans	24	111 1111 11 1					
S. asper	13	11111					
O. acanthium	16	111 11 11					
P. aquatica	19	11111 111 1					
R. crispus	20	111 1111111					
S. oleraceus	38	111					
C. asiatica	47	11111111					
T. repens	48	1111 1 1					
P. dilatatum	39	111 1 1					
B. catharticus	42	11 1					
C. appressa	43	1 1111					
C. glauca	45	111 1					
P. straminea	44	1		1			
J. planifolius	29	1 1					
P. clandestinum	53	1					
P. tricarinatus	51	1	1 1				
I. inundata	49	1					
T. striatum	55	1 11					

Appendix 9 Dendrograms derived from cluster analysis of temporal variations in the composition of 12 species at Transect 1, along the wet meadow transition, Coomonderry Swamp. Correlations of ordination vectors with maximum species and inundation and temperature variables are shown.

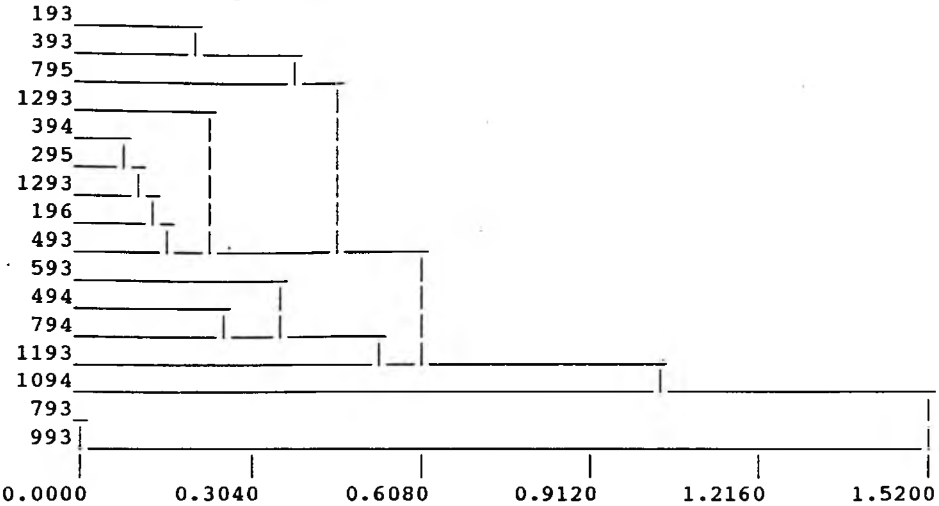
For description of variables and interpretations of dendrograms and ordinations see Section 3.3.3.2 (iii). Temporal samples are named by month and year i.e. '193' is January 1993. Association values are shown along the bottom of each dendrogram. The number of vectors used in each ordination procedure was determined by: (i) the stress value; (ii) differentiation of variables; and (iii) high correlations among vectors. Critical value for correlations (n = 16): $P = 0.001$: $r = 0.742$. $*P < 0.001$.

Isolepis prolifera



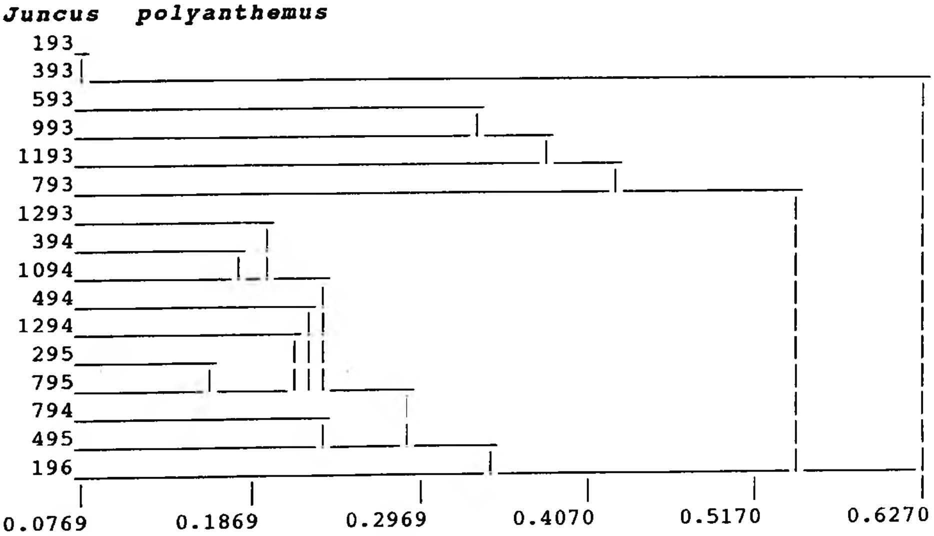
Isolepis prolifera	Vector 1	Vector 2	Vector 3
Relative water's edge	-0.227	0.248	-0.244
Relative water depth	0.331	-0.330	0.161
Relative mean elevation	-0.243	0.296	-0.221
mean monthly minimum temperature	-0.565	-0.327	0.407
mean monthly maximum temperature	-0.589	-0.243	0.392
maximum species	-0.713	0.141	-0.013
2 month lag relative edge	-0.277	0.154	-0.560
2 month lag relative depth	0.257	-0.248	0.560
2 month lag relative mean elevation	-0.222	0.210	-0.570
2 month lag mean monthly min. temp.	-0.293	-0.401	0.197
2 month lag mean monthly max. temp.	-0.412	-0.316	0.147

Pseudoraphis paradoxa



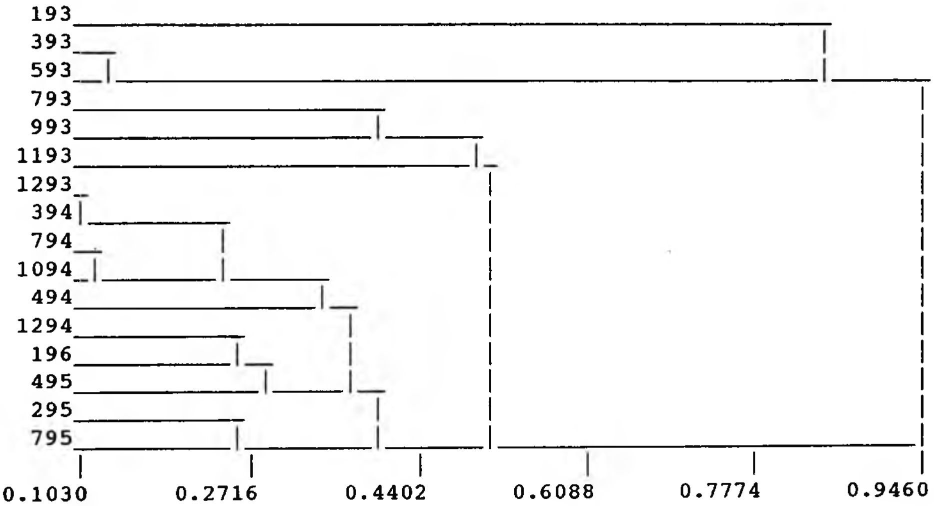
Pseudoraphis paradoxa	Vector 1	Vector 2
Relative water's edge	-0.017	-0.229
Relative water depth	0.149	0.248
Relative mean elevation	-0.025	-0.187
mean monthly minimum temperature	-0.355	-0.467
mean monthly maximum temperature	-0.389	-0.604
maximum species	--0.367	-0.476
2 month lag relative edge	0.022	0.135
2 month lag relative depth	0.054	-0.061
2 month lag relative mean elevation	0.025	0.149
2 month lag mean monthly min. temp.	-0.552	-0.171
2 month lag mean monthly max. temp.	-0.666	-0.300

Juncus polyanthemus



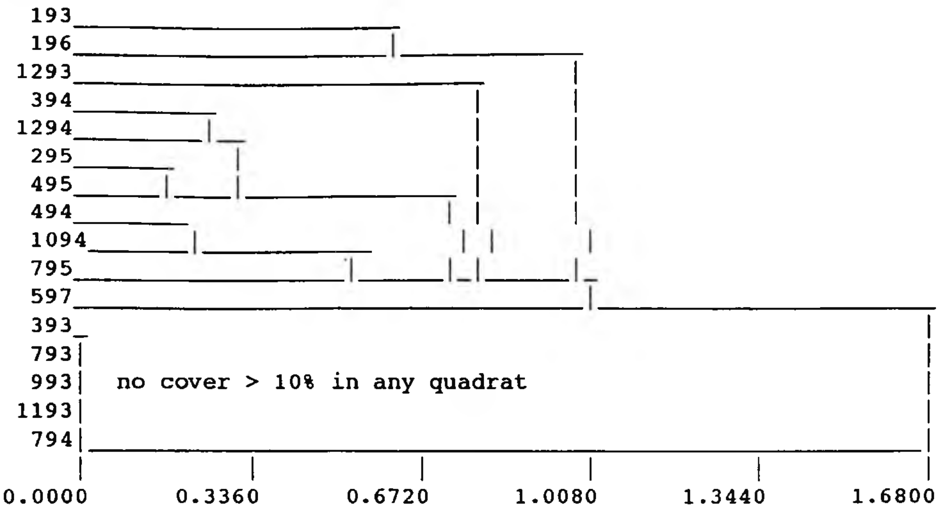
Juncus polyanthemus	Vector 1	Vector 2
Relative water's edge	0.005	0.114
Relative water depth	-0.162	-0.099
Relative mean elevation	0.002	0.133
mean monthly minimum temperature	0.079	0.047
mean monthly maximum temperature	0.182	-0.029
maximum species	-0.360	0.184
2 month lag relative edge	0.067	0.111
2 month lag relative depth	-0.218	-0.053
2 month lag relative mean elevation	0.104	0.033
2 month lag mean monthly min. temp.	0.116	0.409
2 month lag mean monthly max. temp.	0.304	0.361

Juncus procerus



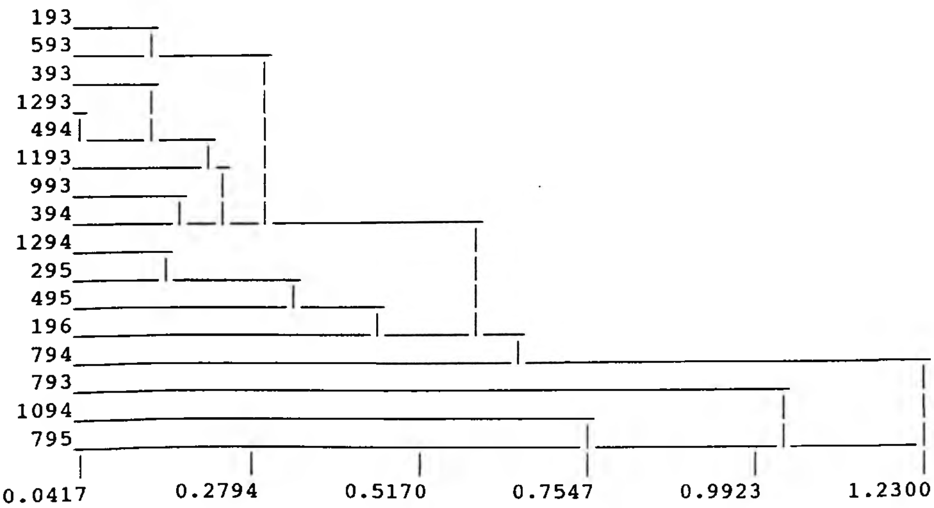
Juncus procerus	Vector 1	Vector 2
Relative water's edge	0.005	0.114
Relative water depth	-0.162	-0.099
Relative mean elevation	0.002	0.133
mean monthly minimum temperature	0.079	0.047
mean monthly maximum temperature	0.182	-0.029
maximum species	-0.360	0.184
2 month lag relative edge	0.067	0.111
2 month lag relative depth	-0.218	-0.053
2 month lag relative mean elevation	0.104	0.033
2 month lag mean monthly min. temp.	0.116	0.409
2 month lag mean monthly max. temp.	0.304	0.361

Paspalum distichum



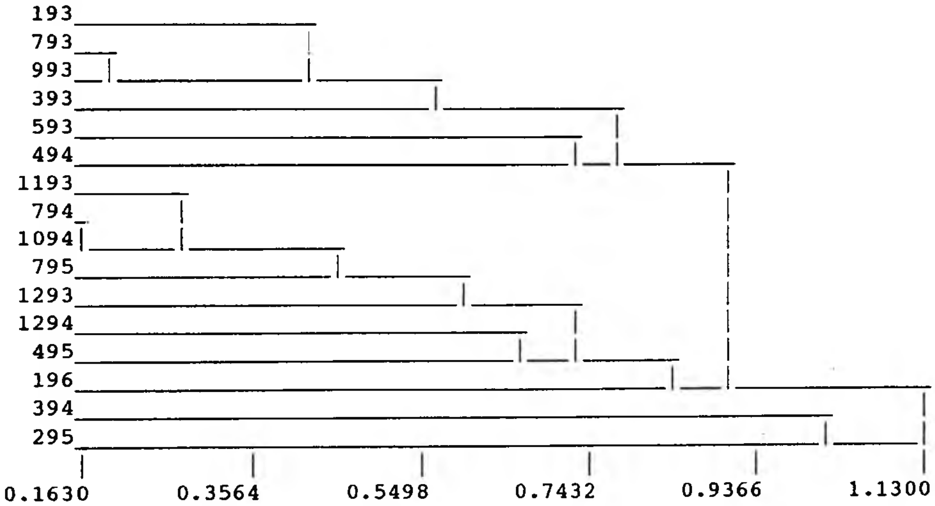
Paspalum distichum	Vector 1	Vector 2	Vector 3
Relative water's edge	0.591	0.196	0.235
Relative water depth	-0.596	-0.149	-0.328
Relative mean elevation	-0.597	0.212	0.230
mean monthly minimum temperature	-0.004	0.310	0.465
mean monthly maximum temperature	0.128	0.256	0.518
maximum species	0.331	0.036	0.480
2 month lag relative edge	0.274	-0.247	0.243
2 month lag relative depth	-0.294	0.399	-0.275
2 month lag relative mean elevation	0.273	-0.351	0.226
2 month lag mean monthly min. temp.	0.236	0.160	0.186
2 month lag mean monthly max. temp.	0.334	0.091	0.294

Marsilea mutica



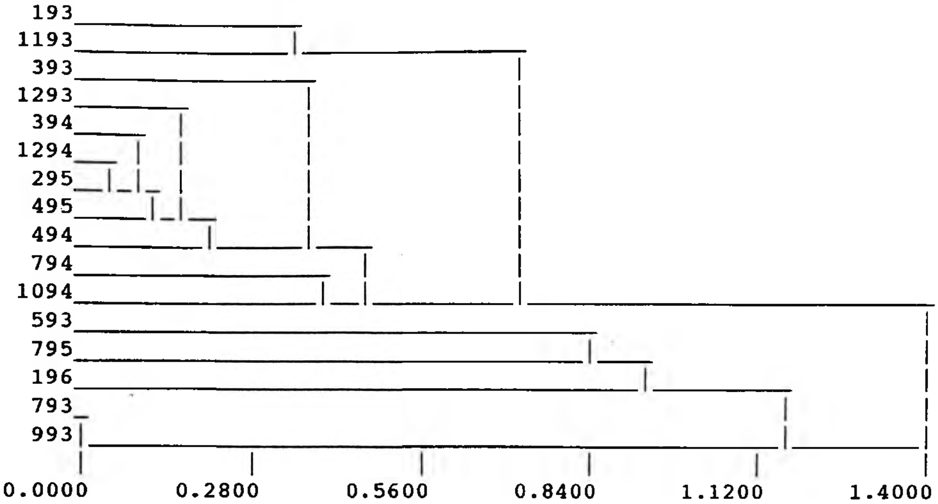
Marsilea mutica	Vector 1	Vector 2	Vector 3
Relative water's edge	0.261	0.056	-0.045
Relative water depth	-0.290	0.064	0.009
Relative mean elevation	0.341	0.037	-0.033
mean monthly minimum temperature	0.294	-0.233	0.415
mean monthly maximum temperature	0.229	-0.376	0.415
maximum species	0.191	-0.215	0.087
2 month lag relative edge	0.053	0.400	-0.131
2 month lag relative depth	0.045	-0.244	0.226
2 month lag relative mean elevation	-0.002	0.348	-0.193
2 month lag mean monthly min. temp.	0.082	-0.092	0.411
2 month lag mean monthly max. temp.	0.041	-0.154	0.301

Ranunculus inundatus



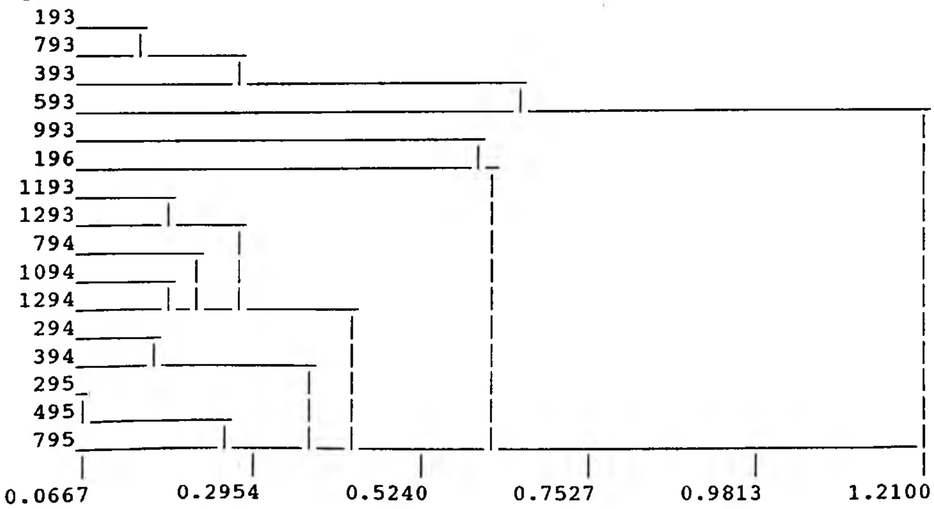
Ranunculus inundatus	Vector 1
Relative water's edge	-0.400
Relative water depth	0.448
Relative mean elevation	-0.423
mean monthly minimum temperature	-0.152
mean monthly maximum temperature	-0.164
maximum species	-0.671
2 month lag relative edge	-0.490
2 month lag relative depth	0.497
2 month lag relative mean elevation	-0.437
2 month lag mean monthly min. temp.	-0.066
2 month lag mean monthly max. temp.	-0.281

Hydrocotyle peduncularis



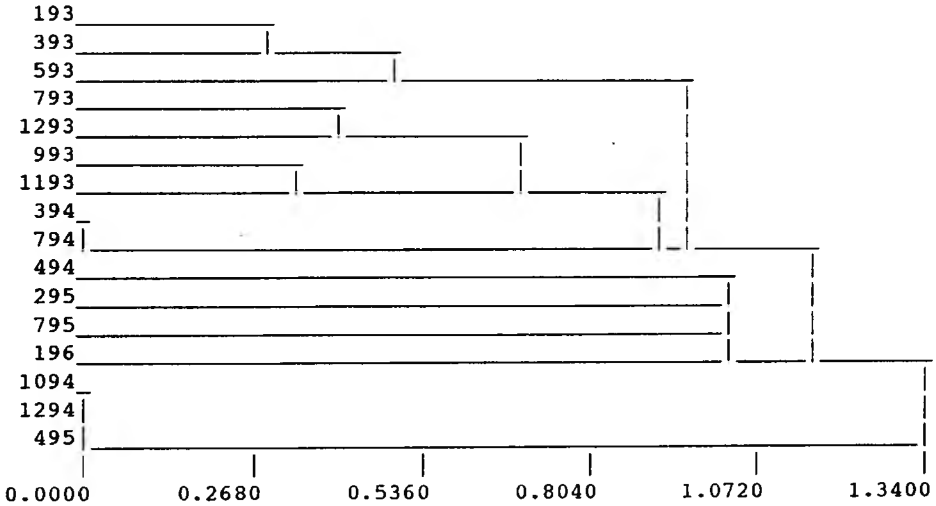
Hydrocotyle peduncularis	Vector 1
Relative water's edge	-0.133
Relative water depth	0.073
Relative mean elevation	-0.164
mean monthly minimum temperature	0.505
mean monthly maximum temperature	0.532
maximum species	0.289
2 month lag relative edge	-0.167
2 month lag relative depth	0.083
2 month lag relative mean elevation	-0.165
2 month lag mean monthly min. temp.	0.285
2 month lag mean monthly max. temp.	0.399

Agrostis avenacea



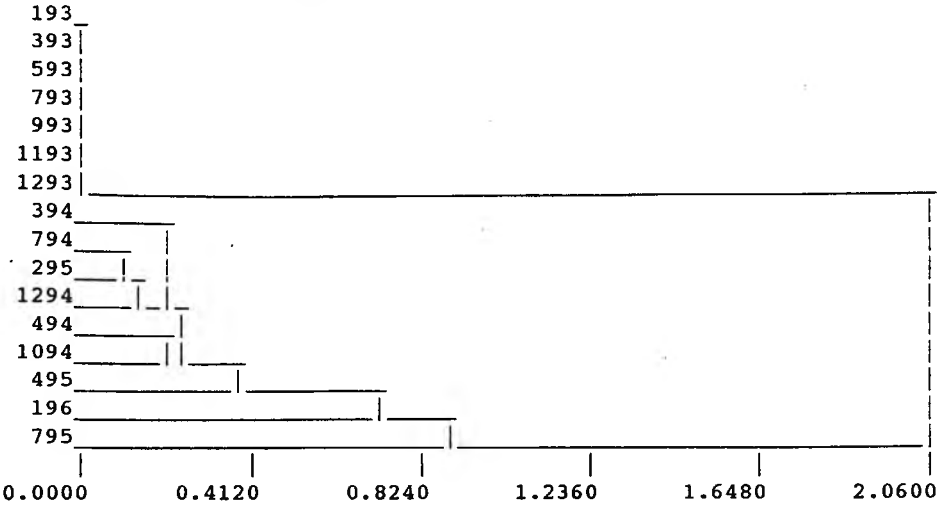
Agrostis avenacea	Vector 1
Relative water's edge	0.048
Relative water depth	-0.183
Relative mean elevation	0.073
mean monthly minimum temperature	0.007
mean monthly maximum temperature	0.103
maximum species	0.316
2 month lag relative edge	0.087
2 month lag relative depth	0.241
2 month lag relative mean elevation	0.157
2 month lag mean monthly min. temp.	-0.149
2 month lag mean monthly max. temp.	0.019

Persicaria decipiens



Persicaria decipiens	Vector 1	Vector 2
Relative water's edge	0.698	-0.327
Relative water depth	**-0.748***	0.328
Relative mean elevation	0.727	-0.285
mean monthly minimum temperature	-0.008	0.563
mean monthly maximum temperature	0.184	0.431
maximum species	0.567	-0.300
2 month lag relative edge	0.222	-0.528
2 month lag relative depth	-0.259	0.585
2 month lag relative mean elevation	0.178	-0.590
2 month lag mean monthly min. temp.	-0.106	0.190
2 month lag mean monthly max. temp.	-0.032	0.074

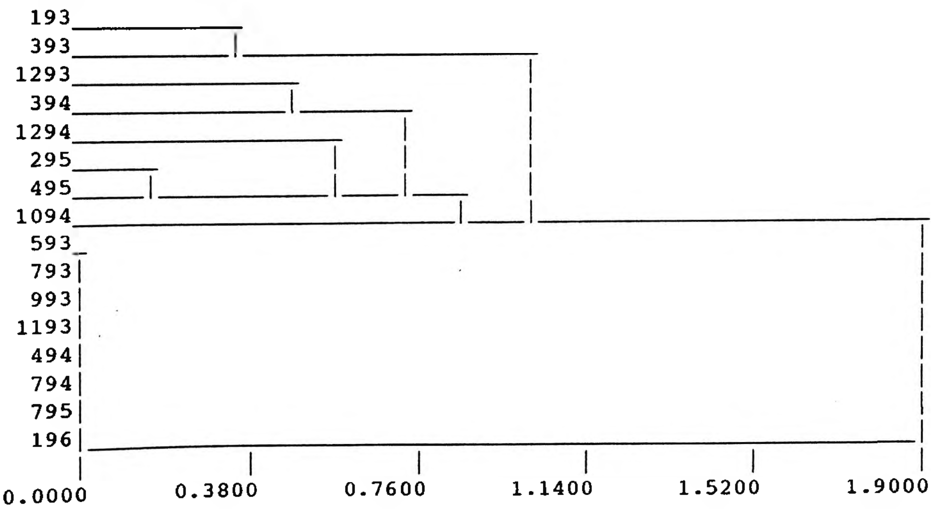
Persicaria praetermissa



Persicaria praetermissa	Vector 1	Vector 2
Relative water's edge	0.250	0.207
Relative water depth	**-0.321**	-0.171
Relative mean elevation	0.334	0.171
mean monthly minimum temperature	0.493	-0.625
mean monthly maximum temperature	0.586	-0.585
maximum species	0.355	0.171
2 month lag relative edge	-0.345	-0.623
2 month lag relative depth	0.400	-0.626
2 month lag relative mean elevation	-0.385	0.662
2.month lag mean monthly min. temp.	0.256	-0.120
2 month lag mean monthly max. temp.	0.223	-0.554

(n = 9) critical value: r = 0.898

Bidens tripartita



Bidens tripartita	Vector 1	Vector 2
Relative water's edge	-0.764	-0.034
Relative water depth	**0.749**	0.070
Relative mean elevation	-0.754	-0.086
mean monthly minimum temperature	0.258	-0.399
mean monthly maximum temperature	-0.001	-0.228
maximum species	-0.554	-0.354
2 month lag relative edge	-0.443	-0.365
2 month lag relative depth	0.450	0.281
2 month lag relative mean elevation	--0.387	-0.285
2 month lag mean monthly min. temp.	-0.119	-0.663
2 month lag mean monthly max. temp.	-0.564	0.301

(n = 10) critical value: r = 0.872

Appendix 10 Proportion of plots with seedlings two months after planting with the seeds of five woody species at two elevations in wet meadow at Coomonderry Swamp

Species	Elevation	Cleared	Uncleared
Eucalyptus robusta	upper	0.47	0.04
	lower	0.91***	0.18*
Casuarina glauca	upper	0.24	0
	lower	0.40*	0
Leptospermum juniperinum	upper	0.49	0
	lower	0.94***	0
Melaleuca ericifolia	upper	0.38	0.02
	lower	0.74***	0
Melaleuca linariifolia	upper	0.57	0
	lower	0.62	0

Proportions of seedlings significantly greater at lower elevation than at upper elevation are indicated (*** $P < 0.001$; * $P < 0.05$ - ChiSq). 'n' plots: cleared: 100 ± 1, uncleared: 50 ± 2.

Appendix 11(i) Mean stem diameters (cm) of saplings after nine months

Species	**Elevation**	**Cleared Weeded**	**Cleared**	**Uncleared**
Eucalyptus robusta	upper	1.65(0.07)^{a}	1.39(0.07)^{ab}	1.29(0.06)^{b}
	lower	1.40(0.06)^{ab}	1.24(0.08)^{b}	1.62(0.06)^{a}
Casuarina glauca	upper	1.32(0.05)^{ab}	1.19(0.04)^{ab}	1.23(0.04)^{ab}
	lower	1.39(0.04)^{a}	1.22(0.05)^{b}	1.33(0.04)^{ab}
Leptospermum juniperinum	upper	1.07(0.05)^{c}	1.05(0.05)^{c}	1.04(0.04)^{c}
	lower	1.37(0.06)^{ab}	1.20(0.06)^{bc}	1.49(0.06)^{a}
Melaleuca ericifolia	upper	0.95(0.03)^{bc}	0.89(0.03)^{c}	0.84(0.03)^{c}
	lower	1.30(0.06)^{ab}	1.12(0.04)^{a}	1.28(0.06)^{a}
Melaleuca linariifolia	upper	0.82(0.03)^{bc}	0.74(0.03)^{c}	0.70(0.03)^{c}
	lower	1.03(0.03)^{a}	0.95(0.04)^{ab}	1.06(0.04)^{a}

Standard errors in parentheses. For each species, means with the same superscripts are not significantly different at P = 0.05 (Tukey Test following ANOVA). Some significant differences indicated by ANOVA (the more powerful test (Zar 1984) were not detected by the Tukey comparison. 'n' plots: 50 ± 4.

Appendix 11(ii) Mean heights (cm) of saplings after nine months

Species	**Elevation**	**Cleared Weeded**	**Cleared**	**Uncleared**
Eucalyptus robusta	upper	106(3)^{a}	100(3)^{a}	98(3)^{a}
	lower	99(2)^{a}	96(3)^{a}	107(3)^{a}
Casuarina glauca	upper	99(4)^{c}	107(4)^{bc}	98(4)^{c}
	lower	127(3)^{a}	119(4)^{ab}	121(4)^{ab}
Leptospermum juniperinum	upper	110(3)^{a}	109(4)^{a}	106(3)^{a}
	lower	113(3)^{a}	110(3)^{a}	117(3)^{a}
Melaleuca ericifolia	upper	82(2)^{b}	83(2)^{b}	81(2)^{b}
	lower	88(3)^{ab}	87(2)^{ab}	94(2)^{a}
Melaleuca linariifolia	upper	73(2)^{b}	69(2)^{b}	68(2)^{b}
	lower	87(2)^{a}	85(2)^{a}	87(2)^{a}

Standard errors in parentheses. For each species, means with the same superscripts are not significantly different at P = 0.05 (Tukey Test following ANOVA). Some significant differences indicated by ANOVA (the more powerful test (Zar 1984) were not detected by the Tukey comparison. 'n' plots: 50 ± 4.

Appendix 12 Species (i) encroaching into cleared plots and (ii) germinating in cleared plots over nine months (December 1994 to August 1995). Data collected at two elevations in wet meadow at Coomonderry Swamp.

(i) Species encroaching into cleared plots:

Triglochin striatum, Lilaeopsis polyantha, Cotula coronopifolia, Ludwigia peploides, Persicaria praetermissa, Persicaria decipiens, Myriophyllum simulans, Isolepis prolifera, Hydrocotyle peduncularis, Ranunculus inundatus, Pseudoraphis paradoxa, Agrostis avenacea, Juncus prismatocarpus, Triglochin procerum, Eleocharis acuta, Phalaris aquatica

(ii) Species germinating from seeds or other propagules (but not vegetative encroachment) in cleared plots over nine months:

Persicaria hydropiper, Persicaria lapathifolia, Persicaria decipiens, Persicaria praetermissa, Bidens tripartita, Echinochloa crus-galli, Fimbristylis velata, Aster subulatus, Centipeda minima, Ludwigia peploides, Conyza albida, Conyza parva, Agrostis avenacea, Sonchus asper, Sonchus oleraceus, Rumex crispus, Hydrocotyle peduncularis, Hypochoeris radicata, Parsonia straminea, Isolepis prolifera, Juncus polyanthemus, Onopordum acanthium, Phalaris aquatica, Senecio madagascariensis, Myriophyllum simulans, Isolepis fluitans, Marsilea mutica, Juncus planifolius, Juncus prismatocarpus, Elatine gratioloides, Philydrum lanuginosum, Paspalum dilatatum, Bromus cartharticus, Cyperus sanguinolentus, Oxalis corniculata, Centella asiatica, Trifolium repens, Veronica plebeia, Callitriche ?stagnalis, Rubus complex, *Isolepis inundata, Euchiton involucratum, Triglochin striatum, Cotula coronopifolia*

Appendix 13 A brief comparison of Coomonderry Swamp to other dunal wetlands of NSW.

There are difficulties in evaluating the importance of Coomonderry Swamp by comparison to NSW north coast wetlands and against the simple criterion of size. Much larger aggregates of wetlands which contain dunal swamps or lakes exist on the north coast, including the Bundjalung complex (17,738 ha), the Crowdy Bay complex (8022 ha), and the Limeburners Creek system (9083 ha) (ANCA 1996). However it is not clear how large some individual wetlands are within these aggregates. In addition, the geomorphologies of many of these complexes are somewhat different (P. Adam pers. comm.). Most occur on extensive dunal swales while Coomonderry Swamp is a more simple hind-dune wetland. Some of the largest dunal lakes of the north coast are deep and hence are not covered in vegetation but do support extensive peripheral vegetation. The largest of these being the two adjoining lakes; Lakes Minnie Water and Hiawatha at 367 ha.

Nevertheless Coomonderry Swamp is by far the largest freshwater coastal wetland in the Sydney Basin and South East Highlands biogeographic regions (these regions are defined by the 'Interim Biogeographic Regionalization for Australia' - 'IBRA') which include the whole of the NSW south coast.

Dunal wetlands are not common on the south coast of NSW. Several dunal water bodies and depressions occur on the Bherwerre Penisula and elsewhere adjacent to Jervis Bay. The largest of these, Lake Windermere fluctuates in size, but would not exceed 45 ha (Norris & Maher 1995). Some small dunal wetlands occurring further south in NSW (B. Timms pers. comm.) have not been well studied.